The Homologies of the Muscles related to the Visceral Arches of the Gnathostome Fishes.

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With Plates 21 and 22 and 1 Text-figure.

In 1874 Vetter published his well-known work on the muscles related to the visceral arches of the Selachii, and, clothed somewhat with Gegenbaur's authority, it immediately became the recognised standard of reference, and all later work relating to the subject has apparently been greatly influenced by it. Certain parts of Vetter's descriptions have, however, always been to me obscure, but I have attributed it to my not being personally familiar with the anatomy of the Selachii. Considering that this familiarity had been in a measure acquired by my present work on the cranial anatomy of Chlamydoselachus, I recently carefully re-read Vetter's descriptions, but I still found the particular parts referred to neither precise nor clear. Tiesing's (1895), Ruge's (1897), and Marion's (1905) later works not helping to a proper comprehension, I then had recourse to dissections of such few specimens of the Selachii, other than Chlamydoselachus, as I had at my disposal. The result has been to lead me to consider the particular parts referred to, in the several works above mentioned, incorrect, and it has also unexpectedly led me to seriously question every one of the several instances cited by Edgeworth (1911) in which one of these visceral-arch muscles of fishes is said to be innervated,

in the adult, by the nerve of a segment of the body other than that from which the muscle itself is developed.

The proof that Edgeworth offers that this change of innervation has taken place in these muscles is: that certain muscles that he finds in embryos are developed from certain segments of the body; that these muscles of embryos are the homologues of certain muscles described by other authors in the adults of the same fishes; and that these latter muscles of the adult are said to be innervated by nerves other than those of the segments from which he (Edgeworth) finds the muscles of embryos developed. If these several premises were all correct, the important conclusion that Edgeworth deduces from them would evidently also be, but it is equally certain that there is the possibility of error in some one of the premises. This seems not to have been given serious consideration, and yet Edgeworth's descriptions of the development of these muscles in the Selachii is markedly different from Dohrn's, to whose important work Edgeworth makes no reference, and it is well known that the innervation of these muscles in the adult has been frequently wrongly or incompletely given. Furthermore, I now find that even the descriptions of the muscles themselves in the adult Selachii are, in certain respects, incorrect.

Certain anatomists hold that a muscle fibre is, from the earliest embryonic stages, connected with the central nervous system by a protoplasmic strand, not yet demonstrable by known microscopic methods, which represents a future fibre of the motor nerve of the segment, or that a "something" (Braus, 1905) else establishes that connection. Other anatomists claim that there is no such connection, and that the motor nerve grows outward, independently, from the central nervous system, and in some unknown way finds its end organ.

According to the first of these two views a nerve should, in normal conditions, innervate a muscle derived from the myotome of its own segment and from that segment only. According to the second view the nerve might, in slightly changed, if not even in normal conditions, find its end organ

in a muscle derived from another segment; and if this change in innervation were then to be transmitted by inheritance, it is claimed that it is fatal to the first-mentioned view (Johnston, 1906, p. 63). There would, however, seem to still be question as to whether this inheritable mutation related to the directive impulse assumed to reside in a nerve fibre, or to a protoplasmic strand, or a something else, that pre-existed and determined the course of the nerve. The mutation might evidently have related to the one or the other. Furthermore, there is frequently question, in the cases cited of such a change of innervation, as to whether the definitive innervation was not in reality primary, being the only innervation that the particular fibres under consideration had ever had in ontogeny, instead of being secondary in the sense of replacing an earlier and normal innervation by the nerve of the segment to which the muscle belongs.

My work, it may here be stated, in no way attempts to solve this vexed and very complicated question. It does however raise serious question as to several of the examples that have heretofore been cited of the so-called secondary innervation of a muscle, and it also quite unexpectedly adds a series of instances in which there must be such an innervation if existing descriptions of the innervation are correct.

Before describing my own investigations, limited to a few Selachii, it will be well to point out some of the inconsistencies and contradictions in earlier descriptions of the development and anatomy of the visceral-arch muscles in these fishes.

Branchial Arches.

Dohrn (1884, pp. 109–115) says that the myotome of each of the branchial arches of selachians, meaning the Plagiostomi, becomes flattened "in the middle," and is finally there separated into two parts, and the descriptions and figures both show that this flattening and subsequent separation takes place antero-posteriorly along a dorso-ventral line passing through the middle of the externo-internal depth of the myotome. The myotome is thus here separated into

deeper and superficial portions, which Dohrn calls respectively the proximal and distal portions of the myotome, proximal meaning nearer the pharyngeal cavity and distal farther from that cavity. The separation of the myotome into these two parts did not apparently extend, in the embryos examined by Dohrn, the full dorso-ventral length of the myotome, for Dohrn definitely says that the dorsal ends of the two portions of the myotome remain attached by a thin intervening portion. The complete separation said to be found in the adult must accordingly take place in later embryonic, or possibly in postembryonic stages.

The cartilaginous bar of the arch, when it first begins to develop, is said by Dohrn to lie against the posterior surface of the proximal portion of the myotome at about the middle of its length, and the bar, as it develops, is more curved than the myotome. The proximal portion of the myotome thus stretches across the morphologically anterior but actually lateral surface of the curved bar, projecting, in the middle of its length, mesial to the bar, and there acquiring a position internal instead of external to it. This middle section of the proximal portion of the myotome is later cut out of the myotome along the line where the myotome crosses the bar, and from the portion so cut out the musculus adductor arcus visceralis is said to be developed. The remainder of the myotome is said to remain external to the branchial bar, and from those parts of its proximal portion that lie dorsal and ventral to the piece cut out to form the adductor, and hence also dorsal and ventral to the curved branchial bar, the musculi interarcualis and coracobranchialis are said (loc. cit., p. 115) to be respectively developed; these two muscles and the adductor thus being primarily continuous and forming the entire length of the proximal portion of the myotome (loc. cit., p. 117).

The dorsal and ventral ends of the myotome, including both its proximal and its distal portions, are each said to bend posteriorly across the dorsal or ventral edge, respectively, of the next posterior gill-pouch (Kiemenspalte), and from that

part of the distal portion of the myotome that lies between these dorsal and ventral bends the musculus interbranchialis is said to be developed. The musculus interbranchialis, as thus defined by Dohrn, is accordingly that part of the distal portion of the continuous myotome that lies in, and extends the full length of, the related branchial diaphragm, that diaphragm being limited dorsally and ventrally by the dorsal and ventral edges of two adjoining gill-pouches. The interbranchialis of the adult Selachii, as defined by Vetter, lies between the dorsal and ventral extrabranchials of the related arch, and the distal ends of these extrabranchials lie, respectively, ventral and dorsal to the dorsal and ventral edges of the next posterior gill-pouch, as will be later fully described, and as is imperfectly shown in Dohrn's figures 1–4, Pl. 7. The interbranchialis of embryos, as defined by Dohrn, is accordingly not the same thing as the one defined by Vetter in the adult. The difference is, in fact, morphologically quite important, although it seems not to have been noticed by Dohrn.

From the distal portion of that part of the myotome that lies dorsal to the dorsal bend in the myotome, Dohrn says (loc. cit. p. 113) that the musculus constrictor superficialis is developed. What is developed from the distal portion of that part of the myotome that lies ventral to the ventral bend is not clearly stated. Dohrn says (loc. cit. p. 114) : "Wie an der dorsalen Seite schlägt sich auch an der ventralen die proximale Portion des Muskelschlauches um die Fortsetzung des Knorpelbogens herum und bildet die tiefen Portionen des Musculus constrictor superficialis (Vetter) ; diesen Namen verdienen sie freilich nur cum grano salis, denn der Constrictor superficialis sollte nur aus denjenigen Muskeln bestehen, welche von den distalen Portionen der ursprünglichen Muskelschläuche abstammen. In der That sind diese Muskeln auch vorhanden, aber in der Vetter'schen Monographie falsch gedeutet worden. Er beschreibt sie als einen Theil der M. Coraco-arcuales, unter dem Namen M. coraco-branchiales ; sie haben aber ursprünglich nichts gemein mit M. coraco-

hyoideus, setzen sich vielmehr nur an sie an, durch eine Fascie von ihn getrennt. Der M. coraco-hyoideus ist ein echter Körpermuskel, aus den Urwirbeln herstammend, und hat genetisch nichts mit der Visceralbogen-muskulatur zu schaffen."

The deeper portion of the constrictor superficialis of Vetter's descriptions, above referred to by Dohrn, is simply a bundle of the proximal fibres of that muscle, and it is thus said by Dohrn to be developed from the proximal portion of the ventral end of the myotome of its arch. But Dohrn has elsewhere definitely said, as just above stated, that this part of the myotome of his embryos becomes the musculus coraco-branchialis. These two muscles must then either have been considered by Dohrn to be identical, or he overlooked the fact that they were both said to be derived from the same part of the myotome. The muscle developed from the remaining, distal portion of the ventral end of the myotome is not specifically named by Dohrn, and although he says that it was wrongly called the coracobranchialis by Vetter, he nevertheless seems to refer to it in a later work (1885) by that name, as will be later shown. How he came to the conclusion that the coracobranchialis of Vetter's descriptions of the adult was developed from this part of the myotome, and that the muscle was wrongly named by Vetter, is not apparent; but it would seem as if it must have been because of Vetter's figure of Acanthias, which seems to show the ventral ends of the constrictores superficiales wholly wanting excepting as they are represented, in the first branchial arch, by a small bundle of muscle fibres. Probably misled by this figure, and Vetter's descriptions of it, which give, as will be later shown, an incorrect idea of the conditions, Dohrn seems to have concluded that the ventral ends of the constrictores must also be wanting in the adult Scyllium, and as he found, in his embryos of that fish, a distal portion of the ventral end of the myotome that had to be accounted for, he concluded that it must be the coracobranchialis of Vetter's descriptions of the adult.

But, whatever Dohrn may have considered to have been developed from the distal portion of the ventral end of the myotome of each branchial arch, it is certain that the musculus interbranchialis was considered by him to be intercalated, in the embryos described by him, between dorsal and ventral muscles, the dorsal one of which, alone, was the constrictor superficialis. This is, however, said by him (loc. cit., p. 144) to be a secondary condition, the constrictor superficialis having certainly, in earlier phylogenetic stages, traversed the related branchial diaphragm along with the interbranchialis; and it is here further said, in direct contradiction to the statement made on p. 113 of his work and above referred to, that the constrictor superficialis is in reality simply the distal portion of the interbranchialis. How it was, or when, the interbranchialis became separated from the portions of the myotome dorsal and ventral to it, or that it ever became so separated, is not said; and as it is definitely said (loc. cit., p. 119) that none of the muscles of the arch are directly inserted on any of the branchial rays, the extrabranchials expressly included, it is certain that these three parts of the myotome were, in the embryos examined by Dohrn, simply arbitrarily established regions of a single continuous muscle.

In the identification, in embryos, of the several muscles above referred to, Dohrn makes frequent reference to Vetter's descriptions of the muscles in the adult Selachii, the evident inference being that, unless otherwise stated, the muscles described by himself, in embryos, were to be considered to be identified with the similarly named ones in Vetter's descriptions of the adult. To this Dohrn makes one exception, the coracobranchialis, which has been above referred to and explained. No limitation or qualification of any kind is made by him in his use of the term musculi interarcuales, and this term is used, where it applies to the muscles of a single arch, both in the plural (loc. cit., p. 113) and in the singular (loc. cit., p. 115). This muscle (or muscles) is said to extend from the pharyngobranchial of an arch to the corresponding element of the next posterior arch, and also ("resp.") to the epibranchial

of its own arch. Reference to Vetter's figures then certainly shows that Dohrn intended to include the musculus interarcualis dorsalis I of Vetter's descriptions in the muscles termed interarcuales by himself, for that muscle is the only one that extends from the pharyngobranchial of one arch to that of the next posterior arch. Fürbringer (1897), however, maintains that the interarcuales dorsales I were not intended by Dohrn to be so included. Fürbringer had previously found (1895) that these musculi interarcuales dorsales I were innervated by spinal or spino-occipital nerves, instead of, as Vetter maintained, by branches of the related branch of the nervus vagus, and he (Fürbringer) proposed for them the name musculi interbasales. In his later work Fürbringer says (1897, p. 406), in making reference to Dohrn's work: "Der Mm. interbasales thut er keine Erwähnung." This is strictly correct, but Dohrn also does not specifically mention either the interarcuales II or III, and it is certain that if so careful a worker as Dohrn had intended to exclude either of these three muscles from the term interarcuales as employed by him he would have definitely said so. This is all the more evident from the fact that, without making reference to these musculi interarcuales I, Dohrn himself says, in the work in question (loc. cit., p. 117), that the musculus subspinalis of Vetter's descriptions, which is simply an anterior member of the interarcuales dorsales I series (Allis, 1915), is probably derived from trunk myotones.

Edgworth says (1911, p. 234) that, in 17 mm. embryos of Scyllium, the lower end of each of the branchial myotomes grows backward and becomes cut off from the remainder of the myotome to form the coracobranchialis. The ventral end of the remainder of the myotome is said to then grow ventrally, external to the Anlagen of the several coracobranchiales, to form the ventral end of the constrictor superficialis. It is then said that: "The upper ends of the myotomes, in embryos between the lengths of 17 and 20 mm., increase in antero-posterior extent, and, fusing together, extend backwards as the trapezius to the shoulder-girdle. Below the Anlagen of

the trapezius each myotome forms a transversely broad plate in the branchial septum. The part internal to the branchial bar forms the adductor; the part external to the bar forms dorsally the arcualis dorsalis, and below that the inter-branchial, whilst the external edge forms the constrictor superficialis." The constrictor superficialis was accordingly developed from that part only of the myotome that lay primarily in the branchial diaphragm, and although a later, ventral downgrowth of this muscle is said to take place, as just above stated, no mention is made of any dorsal upgrowth from that part of the myotome that lies ventral to the trapezius. It is even definitely said (loc. cit., 251) that no levator muscles are developed in the branchial arches of this fish. Here the embryological conditions, thus described, do not agree with the conditions found in a 42 cm. specimen of this fish that I have examined, and which will be later fully described, for in each branchial arch of this fish there is, as in Heptanchus, a dorsal portion of the constrictor superficialis which extends beyond the dorsal extrabranchial and overlaps externally the musculus trapezius. In the hyal arch of embryos of this fish Edgeworth himself describes this dorsal prolongation of the constrictor, and he there not only calls it the levator hyoidei, but says (loc. cit., p. 228) that it is serially homologous with the levator muscles of the branchial arches of the Teleostei. The levator hyoidei is a part of the emuscl Csd_2 of Vetter's descriptions of the Selachii described by him, and as this muscle, in Heptanchus, and in my specimen of Scyllium, certainly has its serial homologues in the dorsal ends of the constrictores of the branchial arches, if the one is the homologue of the levators of the Teleostei the others must evidently also be.

The term "arcualis dorsalis" is said by Edgeworth (loc. cit., p. 226) to be employed by him, as proposed by Fürbringer, to designate the interarcuales dorsalis II and III of Vetter's descriptions, one of which muscles is, however, (Vetter, Fürbringer) an interarcual and not an arcual muscle. The interarcualis dorsalis I of Vetter's description is called

by Edgeworth, as by Fürbringer, the interbasalis. This term I shall also employ in the following descriptions and discussions, the other two muscles being called the arcualis and the interarcualis. The term "interbranchialis" is said by Edgeworth (loc. cit., p. 232) to be employed by him as Vetter employed it, and it is said to lie wholly proximal to the constrictor superficialis.

Dohrn does not specify to what particular fishes his several observations apply, classing them all under the general term "selachians"; but the figures that accompany his work are of Scyllium, Pristiurus, and Torpedo. Edgeworth limits his observations on the Plagiostomi definitely to Scyllium, but in his generalisations he considers them to apply to all the Selachii, and apparently also to the Batoidei. As both authors included Scyllium in their investigations it is instructive to note certain marked differences in their observations. According to Dohrn the dorsal end of each branchial myotome gives origin both to a dorsal portion of the constrictor superficialis and to the interarcuales dorsales of the related arch. According to Edgeworth a dorsal portion of the myotome of each arch is first cut off to form the musculus trapezius, and it is from that portion of the myotome that lies ventral to this dorsal portion that the musculi constrictor superficialis and arcualis (interarcuales, Dohrn) are developed. Dohrn accordingly entirely overlooked the separation of the trapezius from the dorsal ends of the several branchial myotomes, which would certainly be a serious oversight on the part of so careful a worker. According to Dohrn the interarcuales dorsales I are derived from the branchial myotomes, while, according to Edgeworth, they are of spinal origin. According to Dohrn the constrictor superficialis of each arch lies dorsal to the interbranchialis, or possibly both dorsal and ventral to that muscle, and it is definitely said that it does not traverse the branchial diaphragm. According to Edgeworth it is primarily limited to the branchial diaphragm, there lying distal to the interbranchialis; it has no dorsal, levator prolongation and never

acquires it, but it later acquires a ventral prolongation which extends beyond the branchial diaphragm. According to Dohrn the coracobranchialis is formed from the proximal portion only of the ventral end of the myotome of each arch, and the muscle so formed is not the coracobranchialis of Vetter's descriptions of the adults of other Selachii. According to Edgeworth the coracobranchialis is formed from the entire ventral end of the myotome, and it is identical with the muscle described by Vetter. Both authors maintain that the coracobranchialis of Vetter's descriptions is a muscle of branchial, and not of spinal origin.

This comparison of these two embryological works, which are the only ones I know of that pretend to give, in detail, the development of these several muscles, thus certainly shows that the published embryological investigations of these muscles must be accepted with some reserve.

The descriptions of the adult may now be considered.

In the adult Heptanchus the constrictor superficialis of each branchial arch is, as described by Vetter (1874), practically a continuous muscle-sheet with a large angular incisure in its proximal (actually anterior) edge. The dorsal attachment, or origin, of the sheet is said to be partly in a so-called dorsal superficial fascia, but mainly in thin tendinous bands (Platten), which lie external to the musculus trapezius, extend to the dorsal edge of that muscle, and represent the greatly and progressively reduced posterior portion of the superficial fascia above referred to (loc. cit., p. 431). The ventral attachment, or insertion, of the sheet is mainly in a mid-ventral fascia which lies external and ventral to the ventral longitudinal or so-called hypobranchial spinal muscles. The large angular incisure in the proximal edge of the sheet is made by the articulating ends of the epibranchial and ceratobranchial of the arch, and the ends of the muscle fibres, on either side of this incisure, are inserted on those two cartilages. The triangular piece so cut out of the constrictor forms the musculus adductor of the arch, but this

adductor muscle is much smaller than the incisure in the edge of the constrictor.

The innermost (proximal) fibres of the dorsal portions of the constrictores are said by Vetter to have their origins on the inner ends of the "äusseren Kiemenbogen," that is, on the dorsal extrabranchials. It is not said to which arch the extrabranchial related to each muscle belongs, but the use of the expression "äusseren Kiemenbogen," without qualification, and the fact that there is no extrabranchial in the arch posterior to the posterior constrictor (Fürbringer, 1903, p. 432), leads me to conclude that this origin of these fibres of each constrictor is on the dorsal extrabranchial of the arch to which the constrictor belongs. In Heptanchus, the outer (distal) halves of the dorsal extrabranchials are said, in a footnote (loc. cit., p. 409), to be almost completely imbedded in the fibres of the constrictores, and on a later page (loc. cit., p. 429) it is said that: "Die sehr schwach ausgebildeten dorsalen wie ventralen äusseren Kiemenbogen liegen, z. Th. in die Muskeln selbst eingebettet, nahe deren obern und untern Enden auf denselben." This statement that the extrabranchials lie "on" the constrictores is markedly indefinite, but as they usually lie against the posterior surface of the constrictor of the arch to which they themselves belong, and as Vetter says that all of the branchial rays of this fish have that position, one at first concludes that that must also be the position of the extrabranchials. But in one of Vetter's figures (loc. cit., fig 1, Pl. 14), six of these extrabranchials are shown lying one on the anterior surface of each of the six constrictores of the branchial arches, and apparently slightly imbedded in it.

This unusual position of these extrabranchials is one of the points in Vetter's description that I have never been able to comprehend, and as I have two considerably dissected heads of Heptanchus I have examined them with reference to this. In each of these heads the outer (distal) end of the dorsal extrabranchial of each branchial arch lies posterior (internal) to the constrictor of the related arch, as it

normally should. The outer ends of most of the branchial rays of each arch, however, pierce the constrictor of their arch, and from there onward lie against the anterior (external) surface of that constrictor, imbedded in that surface and covered by a thin sheet of connective tissue, which is strongly attached to the anterior (external) surface of the muscle on either side of the branchial ray. The muscle fibres pass unbroken beneath (posterior to) this end of the branchial ray, and none of them are inserted on it. There is no slightest indication that the fibres have been cut in two, and later grown together again. The conclusion is, therefore, inevitable that these branchial rays, in growing outward, have pierced the constrictor, and so passed from its posterior (internal) to its anterior (external) surface; and it seems probable that this is what happened with the extrabranchials in the specimen of this fish examined by Vetter. It is, however, singular that in my two specimens it should be the branchial rays that so pierce the muscle, and not the extrabranchials, while in Vetter's specimen it was the extrabranchials, and not the branchial rays. Vetter's figure is, in any event, misleading, if not actually incorrect, for no part of the constrictor of any of the branchial arches is shown lying anterior (external) to the related extrabranchial.

A deeper (proximal) bundle of the ventral portion of each constrictor superficialis of Heptanchus is said by Vetter to have its ventral attachment, called by Vetter its origin, on a tendinous band related to the dorsal surface of the hypobranchial muscles. Running dorsally from there, this bundle is said to either pass between two of the musculi coracobranchiales of his description, or to perforate one of those muscles, and to be inserted on the ceratobranchial of its arch. This bundle of fibres might accordingly be considered to be a coracobranchialis, and Dohrn did actually so consider it. No musculus interbranchialis is differentiated in this fish.

In Acanthias, as in Heptanchus, the proximal (anterior) fibres of the constrictor superficialis of each branchial arch

are said by Vetter to arise from the inner (proximal) end of the dorsal extrabranchial, but it is here said that it is the extrabranchial of the arch to which the constrictor belongs. The next distal fibres are said to arise from a small and thin tendon which perforates the musculus trapezius and the dorsal trunk muscles to have its insertion on the vertebral column, and the distal and larger part of the fibres to arise from a narrow tendinous aponeurosis which extends dorso-anteriorly from the top of the gill opening next posterior to the muscle. Such a linear aponeurosis is found related to both the dorsal and ventral ends of each of the first four gill openings, and each pair of aponeuroses is said to unquestionably represent the lines where the dorsal and ventral portions of the overlapping outer edge of a long and tall branchial diaphragm, such as is found in Heptanchus, has fused with the anterior (external) surface of the next posterior branchial diaphragm in order to form the small gill openings of Acanthias. It is said that, as a natural consequence of this method of formation of these aponeuroses, the extrabranchials (äusseren Kiemenbogen) lie immediately beneath them, firmly adherent to them. It is not definitely said to which arch the extrabranchial related to a given aponeurosis belongs, but it is said (loc. cit., p. 430) that each aponeurosis marks the limit between the outer, visible, posterior portion of each constrictor (Constr. super. s. str.) and the musculus interbranchialis of the same arch, this latter muscle being covered by the next anterior branchial diaphragm. It is accordingly evident that Vetter considered the extrabranchial that underlies a given aponeurosis to belong to the posterior one of the two branchial diaphragms that have fused to form the aponeurosis.

Each of the linear aponeuroses of Acanthias is thus said to be a persisting cicatrice formed along the line where two adjoining branchial diaphragms have fused with each other, and, that being the case, the cicatrice in each individual fish must evidently have been formed during the life of that particular fish, for that a so-formed cicatrice could have been

acquired, by inheritance, from an earlier form would probably not have been maintained by Vetter. This cicatrice, important as it is, does not involve the dermal tissues, nor are those tissues even said to be adherent to it, as the extrabranchials are said to be. This, in itself, is singular, as is also the fact that whereas the distal fibres of each constrictor, in all the Selachii, Acanthias included, always have, throughout their entire course through the related branchial diaphragms, a course parallel to the free edge of that diaphragm, they are shown by Vetter running nearly at right angles into a line, whether cicatrice or aponeurosis, that is said to represent a part of the former free edge of that particular diaphragm. Vetter has himself called attention to this, and has attempted to explain it, but the explanation is not convincing. Furthermore, the conditions in specimens of Scyllium and Mustelus that I have examined, and that will be later described, are so decidedly opposed to this interpretation of the meaning of the aponeuroses that I consider it wholly impossible that they represent lines where adjoining branchial diaphragms have fused with each other, and, in my opinion, the small external gill openings of Acanthias are due simply to the retarded development of the outer edge of a gill cleft as compared with that of the inner edge of the same cleft.

From the several surfaces of origin above described by Vetter, the fibres of each constrictor superficialis of Acanthias run at first antero-ventrally, and the proximal (anterior) and larger part of them are said to be inserted either entirely (Vetter) on the next anterior aponeurosis, or partly also (Marion, 1905) on the extrabranchial that underlies that aponeurosis. This latter extrabranchial is, according to Vetter's descriptions (loc. cit., p. 430), the one related to the arch to which the muscle belongs. But there is then confusion in the descriptions, for as Vetter has previously said, as just above stated, that certain of the proximal fibres of each constrictor have their origins on the extrabranchial of the arch to which the muscle belongs, these fibres could not have their insertions on that same extrabranchial. The

distal (posterior) fibres of the dorsal part of each constrictor, misleadingly called by Vetter the "untersten" and by Marion the "ventral" ones, are said by both those authors to traverse the branchial diaphragm and to be continuous with the corresponding fibres of the so-called ventral portion of the muscle.

The distal and larger part of the fibres of the ventral portion of the constrictor of each arch are said to have their origins on the linear aponeurosis that extends ventro-anteriorly from the ventral end of the next posterior gill opening. In the first branchial arch, the remaining, proximal fibres of the constrictor, here called by Vetter the "untersten," and by Marion the "median" fibres, are said to have their origins in the mid-ventral line from the tendinous ventral surface of the hypobranchial muscles, and the corresponding fibres in the second to the fourth arches to have their origins from a so-called aponeurosis related to a fascia that lies dorsal to the hypobranchial muscles and serves as surface of origin for them. Running antero-dorsally, the proximal (anterior) and larger portion of the fibres of each constrictor, including the little proximal bundles above referred to, are all inserted on the next anterior linear aponeurosis, while the remaining, distal (posterior) fibres turn dorsally and are continuous with the corresponding fibres of the dorsal portion of the muscle. Excepting only the little bundle of proximal fibres in the first branchial arch, the ventral ends of the constrictores superficiales of this fish thus only reach the dorsal or dorso-lateral edge of the hypobranchial muscles, and comparison with Heptanchus led Vetter to conclude that the ventral ends of the constrictores of Acanthias had undergone marked reduction. He calls especial attention to this, and says (loc. cit., p. 441) that the disappearance of these ventral portions of the constrictores of Acanthias is related to the great development of the hypobranchial muscles, but he makes no mention of what would seem to be a strictly similar disappearance of the larger part of the corresponding dorsal fibres. This assumed disappearance in Acanthias, and also in Scymnus, of

the ventral portion of each constrictor superficialis, is probably, as already stated, what misled Dohrn in his interpretation of the muscles in embryos of Scyllium.

Musculi interbranchiales, not found in Heptanchus, have been differentiated in Acanthias. They are said to be found in each of the first four branchial arches of the fish, but not in the hyal arch. The muscle is said to form a thin muscle-sheet which extends, in each arch, between the extrabranchials and the inner cartilaginous bar of the arch, completely filling the space between them. Marion says that "they are in no sense superficial, nor circular in the same sense that the other muscles are, and they lie in a different plane." Ruge (1897, p. 219) says that they extend from the branchial bar of the arch to the free edge of the related branchial diaphragm, and form the middle part of a "Muskel-Scheidewand," thus lying between dorsal and ventral portions of the muscles of the arch and wholly separating them from each other. Ruge's conception of these muscles is thus totally different from Vetter's and Marion's, but it agrees with Dohrn's description of the muscles in embryos. Vetter says that the interbranchialis of each arch lies close against the anterior (external) surface of the branchial rays of the arch, and extends to the outer ends of those rays, there passing insensibly, without definite boundary, into that part of the constrictor superficialis of the arch that traverses the branchial diaphragm. The distal and larger part of the fibres of each interbranchialis are said to arise, both dorsally and ventrally, in part from the extrabranchial of the related arch and in part from the linear aponeurosis that overlies that extrabranchial, while the proximal (anterior) fibres arise, both dorsally and ventrally, in part from a feeble ligament that extends from the extra-branchial of the arch to the extrabranchial of the next anterior arch, and in part from the latter extrabranchial.

In Mustelus, the proximal fibres of the constrictor superficialis of each branchial arch are said by Tiesing (1895) to arise from a dorsal fascia similar to that described by Vetter in Heptanchus, while the distal (posterior) fibres arise, as in

Acanthias, from a linear aponeurosis, called by Tiesing a septum, said to be formed between it and the corresponding muscle of the next posterior arch. Running antero-ventrally, the proximal (anterior) fibres are said to be inserted on the next anterior so-called septum, while the distal (posterior) fibres traverse the branchial diaphragm and are continuous with the fibres of the ventral constrictor superficialis. The ventral constrictor superficialis of each arch is said to arise from a median ventral superficial fascia, as in Heptanchus, and, running antero-dorsally, to be continuous with the distal fibres of the dorsal constrictor superficialis. No mention is made of any fibres not continuous with those distal fibres of the dorsal portion of the muscle, that large proximal portion of the ventral constrictor that is found in the Selachii described by Vetter thus not being accounted for in these descriptions of Mustelus. It is said that no ventral septum is found in this fish, Mustelus differing in this from Acanthias and resembling Heptanchus. Ruge says that the fibres of the ventral portions of the several constrictores all have a parallel course, and, their edges being contiguous and intimately bound to each other, form a single continuous muscle-sheet.

The so-called septa of Mustelus are said by Tiesing (loc. cit., p. 100) to be formed by the "Verwachsung der Kiemenlöcher" between two adjoining arches, this agreeing with Vetter's conclusion. Ruge (1897, p. 225) also says that these aponeuroses are found "an den Verwachsungsstellen der freien Ränder der Kiemen-Scheidewände." Tiesing says of each septum that, "nach innen und vorn zu befestigt es sich an dem betreffenden Kiemenbogen und schliesst den oberen äusseren Kiemenbogen ein." But it is evidently impossible that a septum, formed where the outer edge of a branchial diaphragm has fused with the next posterior one, could be attached to the inner branchial bar of either of those two arches. Tiesing does not say to which arch the extrabranchial related to a particular septum belongs, but Ruge says (loc. cit., p. 227) that the constrictor superficialis of the

hyal arch of this fish is in part inserted on the extrabranchial of the first branchial arch, which leads one to suppose that that extrabranchial lies beneath the linear aponeurosis related to the first gill opening.

The musculi interbranchiales of Mustelus are said by Tiesing to be practically as described by Vetter in Acanthias.

These several descriptions of these visceral-arch muscles thus, as already stated, do not give a clear and concise idea of the conditions in these fishes, and I have accordingly, as already stated, had dissections made of such specimens of the Selachii as I have at my disposal, which specimens consist of a single already partly dissected head of Triakis, a 42 cm. specimen of Scyllium canicula, and a 43 cm. specimen of Mustelus (species unknown). The accompanying figures show the muscles as found in the two last-named specimens. The musculi constrictores superficiales, interbranchiales, and coracobranchiales were alone particularly considered in the dissections, but other muscles are also shown in the figures. The constrictor superficialis of each arch will be considered as a single continuous muscle, instead of as two separate muscles, one dorsal and the other ventral. I retain the term constrictor superficialis, but, as there is no constrictor profundus, it seems a needless distinction.

In my specimen of Scyllium (figs. 1–7), those portions of the constrictores superficiales of the hyal and first four branchial arches that lie dorsal to the gill openings appear to form, in lateral view, a single continuous muscle-sheet. Immediately dorsal to the gill openings the lines of separation between adjoining constrictores are apparent, and, starting from there, each constrictor can be easily lifted off the next posterior one excepting at its dorso-posterior corner. At that corner each constrictor is inserted on the external surface of the next posterior one, but elsewhere its distal edge simply overlaps and is closely applied to that muscle. Ventral to the gill openings the constrictores are less closely applied to each other, the lines of separation between

adjoining muscles are there distinctly evident, and there is no insertion, at any point, of one muscle on the next posterior one. Both dorsal and ventral to the gill openings there are, in each branchial arch, two or three long muscle strands which start from the internal surface of each constrictor, near the dorsal and ventral ends of the next posterior gill opening, and running respectively dorsally and ventrally, join the muscle strands of the next posterior contrictor. They can, however, easily be lifted off that muscle, and are accordingly not shown, as separate strands, in the figures.

The fibres of the constrictores are everywhere grouped into bundles, which in most places form lamellar bands which occupy the entire thickness of the muscle. Where the muscles are thin these flat bands become simple rounded strands, and they can all be referred to, for convenience of description, as strands of the muscles.

The dorsal edge of the hyal constrictor is nearly straight, and reaches, or lies slightly ventral to, the latero-sensory canal of the body. Its anterior half, approximately, lies anterior to the musculus trapezius and external to the anterior portion of the dorsal muscles of the trunk. Its posterior half lies external to the musculus trapezius, and, at its hind end, overlaps the constrictor of the first branchial arch. The anterior portion of the muscle has its origin in part on the tissues that surround the latero-sensory canal, and in part, ventro-lateral to that canal, on a fascia that is evidently the dorsal superficial fascia of Vetter's descriptions of Heptanchus, Acanthias, and Scymnus. The posterior portion of the muscle has its origin mostly on the external surfaces of the trapezius and the constrictor of the first branchial arch, certain of the tendinous ends of the fibres penetrating those muscles, but it has its origin also in part on ventral prolongations of the tissues that surround the latero-sensory canal of the body. The tissues that surround the latter canal lie directly upon and are firmly attached to the dorsal superficial fascia, that fascia lying directly upon

and being firmly attached to the external surface of the dorsal trunk muscles, and as the line separating the dorsal and ventral trunk muscles here lies considerably ventral to the latero-sensory canal, and hence ventral to the dorsal edge of the trapezius, the fascia lies internal to the latter muscle as well as to the latero-sensory canal. Vetter says that this fascia lies upon the external surface of the musculus trapezius, and he so shows it in his figure of Heptanchus. It lies internal to that muscle in my specimens of Scyllium. There are however, in Scyllium, delicate tendinous lines which lie on the external surface of the trapezius and extend from the dorsal edge of the several constrictores to the tissues that surround the latero-sensory canal, and they apparently represent the tendinous bands (Platten) described and shown by Vetter.

The dorsal edges of the branchial constrictores are all irregular, the most dorsal point of each constrictor lying proximal (anterior) to the distal (posterior) edge of the muscle. From this most dorsal point the dorsal edge of each muscle descends anteriorly, crossing the external surface of the trapezius, and, in the anterior arches, extending ventro-anteriorly beyond the antero-ventral edge of that muscle. Where they cross the trapezius the dorsal edges of these constrictores are inserted on, or firmly attached to, that muscle, certain of the tendinous ends of the muscles penetrating the trapezius. The distal fibres of each constrictor are inserted, as already stated, on the external (anterior) surface of the next posterior constrictor. The distal (posterior) fibres of the fourth branchial constrictor cross the external surface of the shoulder-girdle, and are inserted on the anterior edge of that cartilage along with the fibres of the musculus trapezius.

The dorsal portion of the apparently continuous muscle-sheet that is exposed when the dermis is removed is thus not at all a continuous sheet, and the dorsal edge of the sheet, excepting in its hyal portion, is formed by the dorsal ends of those muscle-strands, only, that lie in the distal portion of

each constrictor. From this dorsal edge of the sheet delicate tendinous lines cross the external surface of the trapezius and extend to the dorsal edge of that muscle, apparently representing, as already stated, the tendinous bands there described by Vetter in Heptanchus.

There are no linear aponeuroses, either dorsal or ventral, related to the gill-openings, but the fibres of the proximal (anterior) half of the hyal constrictor are interrupted, as in many other Selachii, by an aponeurosis that lies approximately in the line of the middle line of the gill-openings. This aponeurosis is attached anteriorly to the mandibular cartilages, and covers the articulating ends of the hyal cartilages.

The muscle strands in the proximal (anterior) portion of the dorsal half of the hyal constrictor run antero-ventrally and are inserted on the ventral half or two-thirds of the hyomandibula, the deeper fibres being shorter than the superficial ones and having their origins on the dorso-lateral edge of the chondrocranium. The proximal fibres of this constrictor thus form a musculus levator hyomandibularis with two heads of origin. The next distal (posterior) strands of the constrictor are inserted in the aponeurosis, just above described, that extends posteriorly from the articulating ends of the mandibular cartilages. The distal (posterior) strands traverse the branchial diaphragm of their arch and are continuous from the dorsal to the ventral end of the muscle. In the dorsal and middle parts of their lengths these distal strands have a nearly dorso-ventral course. Ventrally they spread posteriorly and extend nearly to the ventral end of the shoulder-girdle, there lying external (ventral) to the ventral end of the constrictor of the first branchial arch and external also to the hypobranchial muscles. The strands, excepting a few distal (posterior) ones, all reach the mid-ventral line, and form, with the musculus intermandibularis, a continuous superficial muscle-sheet extending to the symphysis of the mandibulæ. In the posterior three-fifths of this continuous sheet the strands of opposite sides are separated

by a median aponeurotic line. In the anterior two-fifths of the sheet the strands of opposite sides are directly continuous with each other.

A large bundle of the superficial fibres of the ventral portion of the hyal constrictor, composed of a number of muscle strands, separates from the deeper fibres and has its origin on the articular end of the mandibula. Beneath this bundle, and also for a certain distance anterior to it, the deeper fibres of the constrictor have their origins on the ceratohyal, and the so-formed musculus interhyoideus is connected with the adductor mandibulæ by a tendinous fascia which passes internal to the large bundle of superficial fibres and is apparently the homologue of the tendinous fascia described by Vetter, in a similar but wholly superficial position, in Acanthias. Internal to the dorsal edge of this fascia the ligamentum mandibulo-hyoideum has its insertion near the dorsal end of the ceratohyal. Anterior to the large bundle of superficial fibres, the superficial fibres of the continuous muscle-sheet all have their origins on the ventral (morphologically posterior) edge of the mandibula, the line of attachment of the muscle beginning immediately anterior to the tendinous fascia just above described. The anterior portion of this musculus intermandibularis is innervated by a branch of the nervus mandibularis trigemini, and is hence of mandibular origin. The posterior portion is innervated by the nervus hyoideus facialis. The musculus interhyoideus extends to the mid-ventral line and is wholly separate from and independent of the superficial, intermandibularis layer of the sheet. It extends anteriorly slightly beyond the anterior end of the mid-ventral aponeurotic line that separates the constrictor fibres of opposite sides from each other, and is apparently not inserted in that aponeurosis.

The muscle strands of the constrictor of each of the branchial arches all have an approximately dorso-ventral course, and they lie, throughout much the larger part of their length, in the related branchial diaphragm and upon the anterior (external) surface of the next posterior gill-

pouch, separated from it by the branchial and extrabranchial rays of their arch. The fibres that form the distal edge of the muscle, as they cross the dorsal and ventral edges of the next posterior gill-pouch, are strongly attached by connective tissues to those edges, and ventral to the gill opening a certain number of them unite to form a larger strand, which then forms the distal edge of the muscle. By far the larger part of the muscle strands of the dorsal half of the constrictor traverse the branchial septum, only a few of them, one to three strands, being inserted on the epibranchial of the related arch. In the ventral half of the muscle, on the contrary, a considerable number of strands have their origins from the related ceratobranchial, and the additional strands having this origin apparently correspond to those fibres of the dorsal half of the muscle that have been utilised to form the musculi interarcuales dorsales II and III of Dohrn's descriptions, these muscles being represented in Scyllium by a single muscle, the musculus arcualis dorsalis. A few strands of the constrictor have their origins, dorsally, on the dorsal extrabranchial of their arch, near the dorsal bend in the extrabranchial, and a somewhat larger number of strands are inserted, ventrally, on the ventral extrabranchial of the arch, near its ventral bend. All of the fibres of the muscle that lie distal to those thus inserted on the extrabranchials cross the external (anterior) surface of both the dorsal and the ventral extrabranchials and, as shown in the figures, are attached ventrally, by connective tissue, to the external surface of the longitudinal hypobranchial muscles, none of them reaching the mid-ventral line.

Proximal (anterior) to the fibres that have their origins on the dorsal extrabranchial a few strands of the muscle in each arch have their origins in loose connective tissues of the region, and proximal to the fibres that are inserted on the ventral extrabranchial quite a number of strands unite to form a muscle bundle which, as just above stated, corresponds to the musculus arcualis at the dorsal end of the arch. These ventral strands have a different course and insertion in each

of the branchial arches. In the first branchial arch they pass internal (dorsal) to the musculus coracohyoideus, between it and the coracobranchialis I, and end, without reaching the median line, attached to the muscles between which they lie. They pass across the anterior edge of the ventral extrabranchial of their arch at the point where that extrabranchial bends posteriorly around the ventral edge of the next posterior gill-pouch, and they are twisted upon themselves so that their internal surface is presented externally. In the second branchial arch these fibres form a flat band which passes between the coracobranchiales I and II, and reaches the median line. There it is inserted, with its fellow of the opposite side, in a median aponeurosis which passes dorsally between the coracobranchiales II of opposite sides and is continuous with connective tissues that surround the truncus arteriosus and the pericardial chamber. In the third branchial arch the fibres separate into two bundles, one of which passes between the coracobranchiales I and II, and the other between the coracobranchiales II and III. The first bundle does not reach the median line, but the second and larger one reaches that line and is attached, with its fellow of the opposite side, to connective tissues that are attached to the tissues surrounding the truncus arteriosus and pericardial chamber. Certain of those fibres of this muscle that are inserted on the ventral extrabranchial of their arch pass, with that extrabranchial, between the coracobranchiales III and IV; the ventral end of this muscle thus being separated into three parts. In the fourth arch the fibres here under consideration form a flat band which passes dorsal to the coracobranchialis IV and is inserted on the lateral wall of the pericardial chamber, these fibres thus having the relation to the coracobranchiales that the extrabranchial of the arch would have if it were present. The proximal fibres of a constrictor thus tend to acquire a position anterior to the coracobranchialis that is assigned, by nomenclature, to its arch, the extrabranchial of the arch lying posterior to that coracobranchialis. This tendency is the more pronounced the more anterior the arch, and in the

hyal arch the entire ventral end of the constrictor lies anterior even to the coracomandibularis.

Most of the muscle strands of each constrictor lie everywhere anterior (external) to the extrabranchial and branchial rays of their arch, but a few of them are, as above described, inserted on the dorsal and ventral extrabranchials. An angular piece has been cut out of the proximal edge of the primitive constrictor by the articulating ends of the epibranchial and ceratobranchial of the arch, and the cut ends of the muscle fibres are inserted on those cartilages; the angular piece so cut out forming the adductor of the arch, and the dorsal portions of the cut fibres becoming the musculus arcualis dorsalis.

The gill-pouches, with their enclosed branchial lamellæ, are thick, cushion-shaped structures. The external opening of the pouch lies, in a state of repose, at the outer edge of the posterior wall of the pouch, and it is smaller than the internal, pharyngeal opening of the pouch. The dorsal and ventral edges of the pouch are convex, the greatest height of the pouch being in the line of the outer ends of the branchial lamellæ and not at the pharyngeal opening of the pouch. The anterior wall of the pouch curves posteriorly over the distal ends of the branchial lamellæ, and the branchial rays, lying against the anterior (external) surface of that wall, are similarly curved at their outer (distal) ends. The constrictor that lies anterior to a gill-pouch lies on the anterior surface of these branchial rays, and, following the curve in the rays, curves posteriorly over them, the distal portion of the muscle lying in the plane of the external surface of the body, and the proximal portion lying in a plane directed antero-mesially at an angle of about 45° to that surface. The hyal constrictor is not so curved, there being no gill-pouch anterior to it and the cartilaginous bar of the arch lying nearer the external surface than do the bars of the branchial arches.

The posterior wall of each gill-pouch presses against the anterior surface of the constrictor next posterior to it, and forms a slight depression on that surface. The outer edge

of this depression corresponds to the outer edge of the pouch, and not, as might have been expected, to the outer edges of the branchial lamellæ; the lamellæ lying within the pouch and not extending to its outer edges. The constrictor is thinner in the depression than it is immediately beyond it. This, and the insertion of certain of the fibres on the dorsal and ventral extrabranchials of the arch, are the only indications of the differentiation of a musculus interbranchialis.

Dorsal extrabranchials are found in the hyal and first four branchial arches, but ventral extrabranchials only in the first three branchial arches. The dorsal extrabranchial of the hyal arch is a small rod of cartilage lying near the outer, distal ends of the branchial rays, and was not found by either White (1896) or Fürbringer (1903, p. 432) in the specimens examined by them. The dorsal and ventral extrabrachials of the branchial arches lie along the dorsal and ventral edges, respectively, of the depression, just above described, formed on the opposite side of the constrictor of their arch by the pressure of the next anterior gill-pouch. Each of the four dorsal extrabranchials, running dorso-anteriorly from its distal end, reaches the curved dorsal edge of the gill-pouch next posterior to it immediately proximal to the highest point of that edge, and there turns sharply ventrally and but slightly anteriorly over that edge, and then expands into a short spatula-shaped end (Fig. 7) which lies against the posterior surface of the gill-pouch. The dorsal end of each of these dorsal extrabranchials is thus crook-shaped, the crook lying close to the dorsal edge of the constrictor of the arch and embracing the dorsal edge of the next posterior gill-pouch, that pouch there being firmly attached to the extrabranchial by connective tissues. The dorsal half of the flat spatula-shaped end of the first extrabranchial lies against the external surface of the musculus trapezius, closely attached to it by connective tissues, and its ventral half against the external wall of the vena jugularis. The corresponding ends of the other three dorsal extrabranchials lie upon and are strongly attached to the musculus trapezius

alone, the vena jugularis here lying along the antero-ventral edge of the trapezius and partly internal to it.

Each ventral extrabranchial turns posteriorly, at its ventral end, around the ventral edge of the next posterior gill-pouch immediately proximal to the lowest point of that curved edge, and then spreads both anteriorly and posteriorly into long pointed processes. The posterior process hooks around the ventral edge of the next posterior gill-pouch and is prolonged, along the posterior surface of that pouch, by a line of fibrous tissue which lies in the line prolonged of the shank of the next posterior extrabranchial, and is inserted on that extrabranchial at the point where it bends posteriorly around the ventral edge of the gill-pouch next posterior to it. The anterior process of the extrabranchial of the first arch runs antero-mesially between the coracobranchiales I and II, and nearly meets its fellow of the opposite side in the median line, being separated from it by the connective tissues that surround the truncus arteriosus. The anterior process of the extrabranchial of the second arch is similarly related to the coracobranchiales II and III and to its fellow of the opposite side, while the anterior process of the extrabranchial of the third arch is similarly related to the coracobranchiales III and IV, but is separated from its fellow of the opposite side by a considerable interval because of the intervening ventral edge of the pericardial chamber. The antero-ventral ends of these anterior processes of the extrabranchialis approach somewhat the inner branchial bars of their respective arches, especially in the first arch, but they are not especially attached to them by connective or ligamentous tissues. They do not turn posteriorly toward the inner branchial bar of the next posterior arch, and they are not connected with that bar by special ligamentous or connective tissues.

The branchial constrictor that lies anterior to a given gill-pouch, and the related branchial and extrabranchial rays, are all quite strongly attached, by connective tissues, to the anterior wall of that pouch, but the constrictor of the arch

is not so attached, in my specimens, to the posterior wall of the next anterior pouch. The hyal constrictor and its related branchial rays are but loosely attached to the anterior wall of the first gill-pouch, this apparently being due to this muscle being a thicker and stronger muscle than the branchial ones.

On the external surface of each wall of each gill-pouch there are tall and narrow U-shaped lines which mark the lines of attachment of the branchial lamellæ on the internal surfaces of those walls. The loops on the posterior wall of the pouch lie against the anterior surface of the constrictor next posterior to the pouch, and, on that surface of that constrictor, and extending from the outer (distal) ends of the loops to the outer edge of the depression that lodges the gill-pouch, there are, dorsal and ventral to the gill-openings, several strands of a tissue that is largely fibrous, but that shows, under the microscope, certain transverse striæ. These strands are radially disposed, as are the branchial lamellæ; they cross the fibres of the constrictor at right angles, and they are closely attached to the anterior surface of that muscle. Their position suggests both the supporting rods of the branchial filaments in the Teleostomi and the radially arranged muscles related to those rods (Allis, 1903), but it seems improbable that they represent the beginnings of the formation of either of them. On the posterior wall of each gill-pouch, opposite the dorsal one of these two series of fibro-muscular strands, there are one or two flat muscle bands which lie approximately parallel to the fibrous strands, but closely attached to the wall of the pouch instead of to the anterior surface of the constrictor. Distally, these bands pass over the outer edge of the pouch, close to the dorsal end of its external opening, and, turning ventrally, join, near its distal edge, the constrictor that lies along the anterior wall of the pouch. Ventral to the gill-openings similar strands are found, but they here lie upon the internal (posterior) surface of the constrictor next anterior to the pouch, close against the outer edge of the pouch, instead of

on the posterior surface of that pouch (Fig. 3). The action of these fibres, although feeble, must be to retract and constrict the related gill-opening.

The dorsal and ventral edges of the gill-pouches are wholly free, excepting where they are each attached, as already described, to the dorsal extrabranchial of the next anterior arch and to the internal surface of the constrictor of that arch, and there are, as already stated, no linear aponeuroses in any of the constrictores. It is accordingly impossible that the dorsal edges of these pouches, in Scyllium, have been formed by the partial fusion of the edges of a taller gill-opening, as is maintained by Vetter, Tiesing, and Ruge for the Selachii examined by them.

The coracomandibularis, coracohyoideus, and coracobranchialis I all have their origins on the musculus coracoarcualis communis, the other coracobranchiales having their origins on the ventral end of the shoulder-girdle. The coracomandibularis is inserted on the mandibula close to the symphysis, the coracohyoideus on the anterior edge of the ventral surface of the basihyal, the coracobranchialis I on the dorsal surface of the postero-lateral process of the basihyal, the coracobranchiales II–IV each on the hypobranchial of the related arch, and the coracobranchialis V on the ceratobranchial of its arch. There are arcualis, but no interarcualis muscles in this fish, each arcualis being a stout muscle, evidently primarily continuous with the constrictor superficialis of its arch, but lying ventral to the vena jugularis instead of lateral to that vein. The primitive constrictor, in growing dorsally, seems to have been split into two parts when it encountered the vein, one passing ventral and the other dorsal to it.

In the small specimen of Mustelus (Pl. 22, figs. 8–10) the constrictores superficiales of the hyal and branchial arches together present, in lateral view, the appearance, ventral as well as dorsal to the gill-openings, of a single continuous muscle-sheet, the sheet being perforated by the first four gill-

openings and bounded posteriorly by the fifth opening. Both dorsal and ventral to these gill-openings, the muscle strands of the continuous sheet incline posteriorly at a marked angle to the vertical line, this inclination being greater dorsal to the openings than ventral to them, and greater for the posterior strands of the sheet than for the anterior ones. A narrow aponeurotic line extends dorso anteriorly from the dorsal end of each of the four gill-openings that perforate the sheet, but there are no corresponding ventral aponeuroses. Most of the muscle strands on either side of the dorsal aponeurotic lines are juxtaposed, and faint tendinous lines cross the aponeuroses and connect them, this strongly suggesting that the muscle strands were here primarily continuous, and that the aponeuroses are simply tendinous formations, of secondary origin, that interrupt them. The muscle-sheet, in situ, accordingly presents the appearance of being formed by a series of contiguous constrictores, one hyal and four branchial, fused by their adjoining edges both dorsal and ventral to the gill-openings but separated from each other as they pass between those openings. The sheet is, however, not so formed, as will be immediately shown, but this superficial appearance, as it applies to the ventral part of the sheet, is doubtless what led Tiesing to say that, in this fish, the entire ventral constrictor of each arch traverses the related branchial diaphragm and is continuous with the dorsal constrictor.

The anterior edge of the dorsal portion of the sheet is considerably thickened, and this thickened portion is almost completely differentiated, as in Scyllium, as a levator hyomandibularis with two heads of origin, one arising along the line of the latero-sensory canal of the body, continuous with the fibres of the posterior portion of the sheet, and the other from the dorso-lateral edge of the chondrocranium, as Tiesing has already stated. Both portions are inserted, together, on the ventral end of the hyomandibula.

If that part of the muscle-sheet that lies posterior to this levator hyomandibularis be cut along its line of dorsal attach-

ment, or so-called origin, the entire sheet can be turned downward a certain distance, disclosing portions of the dorsal extrabranchials, the dorsal branchial rays of the hyal arch, and the dorsal portions of the five branchial pouches. It is then found that four thin sheets of muscle fibres still attach the large muscle-sheet to underlying structures, and if these thin sheets be cut the large muscle-sheet can be turned downward to the middle line of the gill-openings, as shown in Pl. 22, fig. 9. The entire distal portion of each dorsal extrabranchial is then exposed, and it is seen that they each lie against the anterior (external) surface of the gill-pouch next posterior to the arch to which the extrabranchial belongs, that this distal portion of each of the four branchial dorsal extrabranchials lies slightly posterior to and parallel to the dorsal edge of the gill-pouch next anterior to its arch, and that it extends ventro-posteriorly slightly beyond the level of the dorsal edge of the external opening of the latter pouch. The dorsal extrabranchial of the hyal arch is short, and extends but a short distance along the anterior (external) surface of the first gill-pouch.

The four linear aponeuroses of the large muscle-sheet are now seen to extend entirely through the sheet and to lie one external to each of the four branchial dorsal extrabranchials, attached to them only by loose connective tissues, and comparison with Dohrn's and Edgeworth's descriptions of the differentiation of the musculi adductores in embryos of these fishes definitely shows what the aponeuroses are. According to both those authors those primarily continuous muscle fibres (strands) of the constrictores that cross the inner branchial bars of their respective arches acquire insertion on those bars along the lines where they cross them, and, as a result of this, the musculi adductores are cut out of the primarily long and continuous fibres (strands) so concerned. But before that insertion of these fibres (strands) was acquired it is evident that the individual fibres concerned must first have become tendinous along the lines where they were later to be cut in two, this doubtless being due to the interruption of the

muscle substance of the fibres, because of pressure against the branchial bars, and the consequent formation of a tendinous membrane by the united sarcolemmæ of the fibres so interrupted. This same formation of a tendinous interval, with later insertion, might evidently take place along the lines where the muscle fibres of the primitive constrictores crossed any other skeletal element, and in my specimen of Mustelus it has quite certainly taken place where the fibres of the continuous muscle-sheet crossed the dorsal extra-branchials, the process, with these particular fibres, not being carried to the point of section of the fibres with accompanying insertion on the extrabranchials, while with other fibres this section and insertion has taken place.

The distal end of each extrabranchial lies, as in Scyllium, on the anterior (external) surface of the gill-pouch next posterior to it, and when the dorsal edge of that gill-pouch passes its highest point and turns antero-ventrally toward the pharyngeal opening of the pouch, the extrabranchial also curves antero-ventrally and lies along the edge of the pouch. In each of the branchial arches the proximal end of the extra-branchial then there expands into a flat and thin plate which projects ventrally along the posterior surface of the gill-pouch, there lying either between the pouch and the vena jugularis or between the pouch and the musculus trapezius, the exact relation of each extrabranchial to the vena jugularis and musculus trapezius not being traced. In the hyal arch there is no plate-like expansion of the proximal end of the extrabranchial, this extrabranchial being, as in Scyllium, simply a slender rod of cartilage. In the second, third, and fourth branchial arches each extrabranchial, at the point where it crosses the dorsal edge of the related gill-pouch and curves antero-ventrally along that edge, is somewhat embedded in the musculus trapezius, and it there gives insertion to what appear to be superficial fibres of the trapezius, the number of these fibres increasing progressively from the second to the fourth arches. The fibres so inserted on each extrabranchial lie not only parallel to the fibres of the musculus trapezius, but also in the

lines prolonged of the fibres of the related portion of the musculus interbranchialis of the arch to which the extrabranchial belongs, the latter fibres being inserted on the opposite, ventral, edge of the extrabranchial. In the fourth branchial arch a considerable number of the most proximal fibres of the interbranchialis cross the anterior (external) surface of the extrabranchial of their arch and join the fibres, above described, that appear to form part of the musculus trapezius, lying contiguous with them, along their anterior edge, on the lateral surface of the trapezius. This definitely shows that the fibres that are inserted on the dorsal edge of the extrabranchial are not parts of the trapezius, as they appear to be, but are the dorsal portions of certain muscle strands of the constrictor that have been cut in two by insertion on the extrabranchial, the part ventral to the extrabranchial forming the musculus interbranchialis and the part dorsal to the extrabranchial secondarily fusing with the trapezius.

The musculus interbranchialis of each branchial arch has its origin from that portion of the dorsal extrabranchial of its arch that lies proximal to the point where it begins to curve antero-ventrally along the dorsal edge of the next posterior gill-pouch, and also from somewhat more than half of that part of the same extrabranchial that lies postero-ventral to the curve, and its dorsal edge is seen in fig. 9 lying between the extrabranchial and the dorsal edge of the next anterior gill-pouch. The fibres distal to those thus inserted on the extrabranchial of the arch form the thin sheet of muscle fibres that had to be cut in order to turn the large muscle-sheet of the constrictores superficiales downward as shown in the figure. These distal fibres of each interbranchialis, thus here apparently inserted on the internal surface of the large muscle-sheet, must, in younger specimens, have formed the interbranchial portion of long and continuous muscle strands that passed over the anterior (external) surface of the extrabranchial of their arch and were continued, beyond that extrabranchial, to the dorsal

edge of the muscle. They formed the middle portion, approximately, of each branchial constrictor, and as the constrictores of this fish overlapped each other to a considerable extent, they must have lain internal to certain strands of the next anterior constrictor, and they and the overlying fibres both became tendinous where they crossed the extrabranchial. If, then, those portions of these deeper fibres, or strands, that primarily lay dorsal to the extrabranchial and the related secondarily formed aponeurosis did not abort, they must still persist as a deeper component of the large muscle-sheet.

Ventral to the gill-openings the conditions, aside from the absence of linear aponeuroses, differ in minor details only from those dorsal to the gill-openings. Here each musculus interbranchialis, excepting only a few proximal fibres, is inserted, its full length, on the ventral extrabranchial of its arch, and in each of the branchial arches of my preserved specimen there is a slight fold in the muscle just before it reaches the extrabranchial; the muscle passing, from above, posterior (internal) to the extrabranchial, then turning dorsally upon itself, and then again ventrally to its insertion on the dorso-anterior edge of the extrabranchial (Fig. 10). From the opposite, postero-ventral edge of the extrabranchial a corresponding portion of the fibres of the constrictor of each arch have their origins, and running ventro-posteriorly immediately join, on its internal surface, the continuous muscle-sheet formed by the constrictores superficiales of the several arches. These ventral fibres of the constrictor of each arch thus form a component part of the large muscle-sheet, and they here lie internal to certain fibres of the more anterior arches; but, after crossing the next posterior extrabranchial, they lie between those fibres and certain fibres of the next posterior arch, internal to the ones and external to the others. Here there can be no question as to the persistence of these ventral portions of the fibres of each arch, for they are not here interrupted by linear aponeuroses.

A few of the most proximal strands of the interbranchialis

of each arch unite ventrally to form a small bundle. This bundle contracts to a small and pointed head, which, passing anterior (external) to the ventral extrabranchial of its arch and anterior to the musculus coracobranchialis of its arch, between that muscle and the next anterior coracobranchialis, is inserted on the dorsal surface of the hypobranchial muscles. These bundles are always referred to, in all descriptions of these muscles, as parts of the musculi interbranchiales, but it is to be noted that they are in reality the ventral ends of continuous dorso-ventral fibres of the constrictores, no interbranchiales having been cut out of these particular fibres by insertions on the extrabranchials. Convenience of description, however, requires that they be considered to form parts of the interbranchiales. The more distal strands of each musculus interbranchialis extend either from the dorsal to the ventral extrabranchial of their arch, or from the related dorsal linear aponeurosis to the ventral extrabranchial, lying along the anterior (external) surface of the branchial rays of the arch, between those rays and the posterior wall of the next anterior gill-pouch. Certain of the branchial rays, in certain of the arches, have cut through the muscle in places, and there give insertion to the cut ends of the fibres.

The coracohyoideus and coracobranchialis I are both inserted on the basihyal, the coracobranchiales II, III, and IV each mainly on the hypobranchial of the related arch, but also partly, in arches II and III, on a small cartilage interpolated between the hypobranchial and ceratobranchial, and corresponding, in position, to the most dorsal one of the three cartilages marked Hbr II in Fürbringer's figures of Torpedo ocellata (1903, Fig. 21, Pl. 17). In the fourth arch this independent cartilage has either fused with the ventral end of the ceratobranchial or has not separated from it, and the coracobranchialis is accordingly there partly inserted on the ceratobranchial. In the first branchial arch the cartilage is found lying between the ventral end of the ceratobranchial of that arch and the basihyal. The most anterior hypobranchial is related to the second branchial arch, as shown in Fürbringer's

several figures, and not to the first arch, as shown in Gegenbaur's (1872) figure of Galeus. The coracobranchiales I and II arise from the dorsal surface of the hypobranchial muscles, but the coracobranchiales III, IV, and V from the lateral surface of the pericardial chamber.

An angular piece has been cut out of the proximal edge of each constrictor, as in Scyllium, to form the musculus adductor of the arch, and the cut ends of the fibres are nserted on the related epibranchial and ceratobranchial.

In the large head of Triakis, the muscles were only superficially examined. The constrictores superficiales here, as in Mustelus, form a continuous muscle-sheet perforated by the first four gill-openings, and there are dorsal aponeuroses, but no ventral ones. The dorsal aponeuroses are not so well developed as in my specimen of Mustelus, certain of the superficial muscle strands of the constrictores crossing the aponeuroses, and others there being simply pinched, without being completely interrupted. The aponeuroses here seem to have been in part formed by the invasion of subdermal connective tissues, rather than by the interruption of the muscle substance of the fibres. Where the fibres of the hyal constrictor cross the extrabranchial of that arch the fibres are also partially interrupted, and the beginning of the formation of a linear aponeurosis is plainly evident; and here there is no invasion of connective tissues. That part of each constrictor that lies dorsal to the dorsal extrabranchial of its arch, excluding the first branchial arch, joins, as in Mustelus, and even more markedly so, the musculus trapezius.

Comparing the conditions in Scyllium, Mustelus, and Triakis, as above described, with those described by Vetter in Heptanchus, it is certain that the continuous muscle-sheet formed by the constrictores superficiales in Mustelus and Triakis has arisen by the fusion of the separate but overlapping constrictores of Scyllium and Heptanchus. To

what extent these overlapping and fused muscles have each been preserved, or have aborted, is problematical; but it is certain that the several sections of the continuous muscle-sheet that are included between each two of the series of dorsal aponeuroses each contains elements derived from at least two adjoining arches. In my specimen of Mustelus certain of the fibres of the constrictor of the hyal arch even cross, in their dorso-posterior course, all of the dorsal extra-branchials of the fish, including the somewhat rudimentary extrabranchial of the hyal arch. Those portions of the fibres of the constrictores of Mustelus and Triakis that lie ventral to the ventral extrabranchials are not interrupted by linear aponeuroses, and there is hence no reason to suppose that they there aborted, or even became tendinous. They must simply have joined the overlying fibres of the continuous muscle-sheet and persisted as part of it. There is, however, no noticeable evidence of any thickening of the sheet at these places. The muscle-sheet is, on the contrary, much thicker in its anterior portion, where there is no overlapping of these muscles, than in its posterior portion, where this overlapping takes place.

This interpretation of the constrictores in these several fishes, based wholly on anatomical investigation, finds unexpected confirmation in Dohrn's figures of sections of embryos said to be of Scyllium canicula (1884, Figs. 1–4, Pl. 7). In those figures Dohrn shows the constrictores superficiales overlapping each other to such an extent that three, or even four, of them may be superimposed the one above the others, and certain of them are even shown fused with each other to form a single muscle-sheet. How sections of a selachian, with the constrictor muscles arranged as described by Dohrn, Vetter, and others, could be sectioned so as to show these muscles in this relation to each other has heretofore been to me incomprehensible, but sections of a fish in which these muscles were as I have above described and interpreted them in Mustelus could easily be sectioned to show them as given in Dohrn's figures. It is, however, to be particularly

noted that in my specimen of a small but adult Scyllium it would be impossible to cut a section that could show the conditions given by Dohrn in embryos of that fish. The constrictores superficiales of this fish are so nearly dorso-ventral in position in their dorsal portions that no one of them overlaps more than the next posterior muscle, the gill-pouches elsewhere intervening and separating the muscles; and in their ventral portions the constrictores do not at any point fuse with each other, as Dohrn definitely shows them in his sections.

In the adult specimens of Acanthias and Scymnus that were examined by Vetter and Marion, conditions strictly similar to those above described in Mustelus and Triakis must certainly have existed, but they were misinterpreted by those authors. Minor differences, however, apparently exist, as in Acanthias, where it would seem, from Vetter's descriptions, as if the dorsal fibres of the constrictor of a given arch, had largely aborted after they had crossed the extrabranchial of the next posterior arch, had still more largely aborted after crossing the extrabranchial next posterior to that one, and had wholly aborted on reaching the third posterior extrabranchial.

The constrictores superficiales of Mustelus, Triakis, Acanthias, and Scymnus, and of all other Selachii where the conditions are similar, thus forming a continuous muscle-sheet which is subdivided, by the transverse aponeuroses, into what appear like several separate segments, the question of the innervation of these several segments becomes important. Vetter says that he could not satisfactorily determine the innervation of these muscles in the branchial arches either of Acanthias or Scymnus, but in the hyal arch of those fishes he limits the distribution of the branches of the nervus facialis strictly to the constrictor of that arch, as that constrictor is defined by him. Tiesing says that, in Mustelus, the branches of the nervi glossopharyngeus and vagus are distributed only to those segments of the dorsal portions of the constrictores of that fish that are included

between the corresponding linear aponeuroses, while in the ventral portions of the muscles, where there are no aponeuroses to interrupt the muscle fibres, those fibres are innervated, their entire lengths, by the nerve of the related arch. Ruge shows all those fibres of the hyal constrictor that are not interrupted by the most anterior linear aponeurosis continuing onward to the dorsal edge of the continuous muscle-sheet, and his descriptions lead one to conclude that these fibres are innervated, their full lengths, by the nervus facialis, while the fibres interrupted by the aponeurosis are only so innervated up to the aponeurosis.

If the innervations thus ascribed to these muscles by Vetter, Tiesing, and Ruge are correct, and if my conclusions regarding these muscles are also correct, the constrictores superficiales of all fishes in which they are interrupted by linear aponeuroses thus unexpectedly present typical examples of a muscle derived from one segment of the body being innervated by the nerve of another segment; and here, not only would the innervation be definitely a secondary one, replacing an earlier and normal innervation, but the change of innervation would have taken place in definitely postembroyonic, if not in practically adult, stages. Furthermore, the secondarily acquired innervation of different parts of the dorsal strands, or fibres, of the constrictores of the hyal and first branchial arches of Mustelus would be by several different nerves, while the ventral portions of those same strands, or fibres, would be innervated by a single nerve. This certainly seems improbable, if not impossible, and until Vetter's, Tiesing's, and Ruge's statements have been properly controlled, it seems proper to conclude that the innervations given by them are incorrect, and that the muscle of each arch retains its primitive and normal innervation. That certain individual fibres of each constrictor are cut in two where they are crossed by the linear aponeuroses is practically certain, and in all such cases it is probable that that part of each muscle fibre that thus lost its connection with its motor nerve underwent paralysis and subsequent reduction,

or abortion ; this then in part accounting for the absence of any undue or noticeable thickenings in the overlapping portions of the muscles.

In the Batoidei, as in Acanthias and Scymnus, the continuous muscle-sheet formed by the constrictores superficiales is said to be separated by septa into separate muscle segments, which are assigned one to each branchial arch and one to the hyal arch ; but it is impossible to definitely determine, from the descriptions, whether or not these so called septa of the Batoidei are similar to the linear aponeuroses of the Selachii. Dohrn's figures (1884, Pl. 7, figs. 5 and 6) of sections of embryos of Torpedo would lead one to conclude that dorsal to the gill-openings the conditions were as in Mustelus, while ventral to the opening the primitive constrictor of each arch turned posteriorly and fused with the external surface of the next posterior constrictor, not passing beyond the line of that contact and fusion. The ventral septa, at least, of this fish would then not be similar to those in the Selachii. There is, however, certainly some error in the descriptions of these fishes, for it is evident that the constrictor superficialis of a given branchial arch could not lie anterior to the gill-opening between that arch and the next anterior one, and yet that is the position that these muscles have in both Tiesing's (1895) and Marion's (1905) figures of these fishes.

The musculi trapezius, coracobranchiales, and adductores arcuum branchialium may now be more particularly considered.

Of the trapezius Edgeworth says (1911, p. 257) : "Levatores arcuum branchialium are developed from the upper ends of the branchial myotomes in Teleostomi, Ceratodus, and Amphibia, but are not developed in Scyllium, Sauropsida, rabbit and pig. The method of development of the trapezius —apparently a homologous muscle throughout the vertebrate groups—is intimately related to these differences. It is developed in Teleostomi and Amphibia from the fourth, in Ceratodus from the fifth, levator, i. e. from the penultimate or ultimate levator ; whereas in Scyllium, Chrysemys, Gallus

and rabbit, it is formed from the upper ends of the branchial myotomes—five in Scyllium, four in Chrysemys, two in Gallus, and three in the rabbit. In view of the facts that in Scyllium the subspinalis and interbasales, developed from trunk-myotomes, are attached to the pharyngobranchials, and that the trapezius is innervated only by the XIth—the most posterior of the vagus roots—even though a constituent from the glossopharyngeal (first branchial) segment takes part in its formation, it is probable that the absence of levatores and associated method of development of the trapezius in Scyllium, Sauropsida, and rabbit are secondary phenomena, and that the primitive condition is a series of levatores formed from the uppermost portions of the branchial myotomes."

The trapezius is thus said by Edgeworth to be a muscle that is wholly of branchial origin but that varies greatly in the branchial myotome or myotomes from which it is derived, and in the adult Scyllium, at least, it is definitely stated that the muscle is innervated by the eleventh nerve alone. It is also elsewhere definitely stated (loc. cit., p. 281) that muscles derived from the trapezius are innervated in Lacerta by spinal nerves alone, and in Gallus and the rabbit both by the eleventh nerve and by spinal nerves; and frequent references to the trapezius being innervated by the eleventh nerve, or by the eleventh spinal, leads one to conclude that Edgeworth considered the muscle to be innervated by that nerve, or by spinal nerves, in all vertebrates. The muscle is, accordingly, one of those to which I made reference in the opening paragraph of this paper as being said by Edgeworth to be innervated by the nerve of a segment of the body other than that from which the muscle is developed. The condition of this muscle, as found in the adults of fishes, does not, however, warrant this conclusion in so far as it applies to them.

In the adult Heptanchus certain fibres of the trapezius are said by Vetter to be inserted on the branchial bar of the most posterior, or seventh, branchial arch, the remaining fibres of the muscle being inserted on the shoulder-girdle. Between the seventh branchial bar and the shoulder-girdle

there is no gill-opening, and no musculus constrictor superficialis is described in relation to this seventh arch.

In the adult Chlamydoselachus I find conditions strictly similar to those in Heptanchus, excepting that in this fish there are but six branchial bars and six gill-openings, the sixth gill-opening lying anterior to the sixth branchial bar. The distal, ventro-lateral end of the so-called epipharyngobranchial of the sixth arch lies close to the shoulder-girdle, and that bundle of the trapezius that has its insertion on that element of this arch extends nearly to its hind end. The insertion of the trapezius on the shoulder-girdle begins opposite the hind end of the sixth epipharyngobranchial, and from there extends upward along the anterior edge of the shoulder-girdle. The trapezius is overlapped externally by the dorsal ends of all of the constrictores superficiales, including the constrictor of the fifth branchial arch, and each of the five branchial constrictores is similarly overlapped by the next anterior constrictor, the muscles thus being, in this respect, serially homologous.

In Acanthias and Scymnus the trapezius, as described by Vetter, resembles that in Heptanchus and Chlamydoselachus excepting in that its relations to the branchial bars are modified by there being but five branchial arches in these fishes, and in that the trapezius is here perforated by the slender tendons that are said to alone represent the dorsal portions of the four branchial constrictores superficiales. In the adult Mustelus the trapezius is said by Tiesing to closely resemble that in Acanthias, as described by Vetter, and Tiesing makes no mention of any fibres of the constrictores superficiales joining the trapezius, such as I find in my young specimen of this fish. In Chimæra (Vetter, 1878), there are minor, and for my purpose, unimportant variations in the muscle.

In Heptanchus and Chimæra, Vetter could not determine the innervation of the trapezius, but Fürbringer (1897) has since shown that in Heptanchus it is innervated by branches of the nervus vagus. In Acanthias and Scymnus the muscle

is said by Vetter to be innervated either by branches of the nervus intestinalis vagi, or, possibly, by that nerve together with delicate branches of other, more anterior portions of the vagus. In Prionodon glaucus, that anterior bundle of the trapezius that has its insertion on the branchial bar of the ultimate arch of the fish is said by Vetter (1878, p. 460) to be innervated by a branch of the nervus vagus quartus, the remainder of the muscle being innervated by the nervus intestinalis vagi. In Chlamydoselachus I find the muscle innervated by a branch of the vagus that lies next posterior to that branch of the nerve that is sent to the penultimate branchial arch.

The anatomical evidence regarding this muscle in these several fishes, taken by itself, would thus evidently lead to the conclusion that the trapezius, in each of the fishes considered, is simply a differentiation of the constrictor superficialis of the ultimate branchial arch of that particular fish—the seventh in Heptanchus, the sixth in Chlamydoselachus, and the fifth in Acanthias, Scymnus, and Mustelus—or, possibly, of that arch and other more posterior arches if such arches primarily existed and have successively disappeared by reduction or transformation. This conclusion would then differ from that arrived at by Vetter (1874, pp. 432–433) only in that the trapezius is considered to be derived mostly, or entirely, from the constrictor of the ultimate persisting branchial arch instead of from the constrictor of a modified and more posterior arch that is represented in the shoulder-girdle. This derivation of the muscle would also explain, and find confirmation in, Dohrn's otherwise inexplicable failure to find it developed from the dorsal ends of all of the branchial myotomes, as Edgeworth maintains that it is developed; and the partial fusion of the proximal fibres of the dorsal portions of the constrictores superficiales of the second to the fourth branchial arches with the trapezius, in my specimens of Mustelus and Triakis, would probably explain how Edgeworth came to consider the latter muscle to be developed from the dorsal ends of all of the branchial myotomes. It is, however,

to be noted that this partial fusion of these fibres with the trapezius is not found in my specimens of Scyllium, and it is to embryos of this particular fish that Edgeworth's descriptions relate. This view of the development of the trapezius from the constrictor of the ultimate branchial arch is also in fullest accord with Greil's very complete descriptions of its development in Ceratodus.

In this latter fish, Ceratodus, a muscle called by Greil the dorsoclavicularis is said by that author (1913, p. 1343) to represent the phylogenetic beginning of a musculus trapezius. This dorsoclavicularis is said by Greil (loc. cit., p. 1139) to be derived from a ventral process of the posterior half of the second trunk myotome, which, forking over the fifth branchial cleft, sends one process down anterior to that cleft and the other posterior to it. The former process lies in the fourth branchial arch, and from it is developed the axial mesoderm of that arch. The posterior process is shown in Greil's fig. 1, plate 52, apparently lying posterior and partly internal to a branchial pouch which is called, in the index lettering, the "siebenten Schlundtasche," that is, the sixth branchial pouch. In figs. 3 and 4 of the same plate the process is shown lying directly external to this sixth branchial pouch, close against the posterior edge of the fifth branchial cleft. The sixth branchial pouch never breaks through to the exterior.

The posterior fork of the ventral process of the second trunk myotome of Ceratodus accordingly lies in the fifth branchial arch alone, or both in that arch and the region of a sixth branchial arch that never develops. The process is said to separate into superficial and deeper portions. The deeper portion grows inward, dorsal to the pericardium, and forms a muscle which, although lying ventral to the pharyngeal cavity, is called the musculus dorsopharyngeus. This large muscle is the exact serial homologue of a smaller muscle, called the interbranchialis IV, which is developed from the ventral end of the axial mesoderm of the fourth branchial arch; and both these muscles, lying dorsal to the pericardial cavity and the truncus arteriosus, are serial

homologues of the so-called musculi interbranchialis posterior, interbranchialis anterior, and ceratohyoideus, which are developed, respectively, from the ventral ends of the axial mesoderm of the third, second, and first branchial arches, but lie anterior to, and hence morphologically ventral to, the truncus arteriosus.

The superficial portion of the posterior fork of the ventral process of the second trunk myotome grows ventrally external and ventral to the pericardial cavity, and apparently separates into three muscles, but there is some confusion in the name given to them. One of them is certainly the musculus clavicularis, or dorsoclavicularis, which, as above stated, is said by Greil to represent the phylogenetic beginning of a musculus trapezius (den ersten phyletischen Anfang eines Trapezius höher stehenden Formen). The second and third muscles are first called the dorsobranchialis and dorsohypobranchialis, but later the names dorsobranchialis, dorsocleidobranchialis, coracocleidobranchialis, cleidobranchialis, and coracobranchialis are apparently used either to designate those muscles themselves or muscles derived from them.

The musculi dorsopharyngeus and dorsoclavicularis are definitely said by Greil (loc. cit., p. 1249) to be innervated by a branch of the nervus vagus given off close to the ramus intestinalis vagi. The other muscles derived from the ventral process of the second trunk myotome must then also, in embryos, be innervated by the vagus, but I do not find that this is so definitely stated. A muscle that Greil considered to be the homologue of the trapezius is, in any event, said by him to be derived from the axial mesoderm of the fifth (or fifth and sixth) branchial arch, and it is innervated by a branch of the nervus vagus that has the position, serially considered, of a nerve of that arch (or arches).

Froriep (Greil, 1907, Discussion) thinks that this origin of the axial mesoderm of the fourth and fifth branchial arches of Ceratodus from a trunk myotome needs confirma-

tion, and Edgeworth (loc. cit., p. 176) also questions it, but as it is a question that relates primarily to the origin of the mesoderm of these two arches, and involves that in the other visceral arches also, the question of a secondary change in the innervation of a muscle, as I am at present considering it, is not involved.

Edgeworth (loc. cit., p. 243), in his own investigations, finds the trapezius of Ceratodus "proliferated from the outer side of the fifth levator" arcus branchialis; these two muscles together thus strikingly recalling the trapezius of the adult selachian. This origin of the muscle is thus in accord with my contention that it is developed from the primitive constrictor of the ultimate branchial arch of the fish, and from that constrictor only, and that it accordingly retains, in the adult, its normal and primitive innervation.

In the Teleostomi the conditions are probably strictly comparable to those in Ceratodus, but this cannot be definitely established from the descriptions given. Edgeworth says that the trapezius is developed, in all these fishes, from the fourth levator arcus branchialis. In Amia it is said (loc. cit., p. 239) to be represented by the fifth external levator of my descriptions of that fish, a muscle that I found innervated (Allis, 1897, p. 696) by a nerve that arose either from the base of the post-trematic branch of the third vagus nerve (nerve of the fourth branchial arch), or from the main trunk of the vagus near the base of that vagus nerve. In Acipenser the muscle is said by Edgeworth (loc. cit., p. 236) to be found in 8½ mm. embryos, given off from the fourth levator, but to be in process of disappearing in 11 mm. embryos. In the adult it is said, on Vetter's authority, to be absent. The fifth levator of Vetter's descriptions of this fish is said to be developed from the fifth branchial myotome, and although it persists in the adult, it is not considered by Edgeworth to represent the trapezius, as it does in Amia. This seems singular, for in Polyodon there is a well developed trapezius (Danforth, 1913, p. 141), innervated by a branch of the vagus, and but four levatores arcuum branchialium;

the trapezius thus apparently representing the fifth levator. In Menidia, Herrick (1899, p. 117) found a trapezius innervated by a branch of the vagus, and there are but four levatores in that fish. In Scomber I found (Allis, 1903, p. 207) five external levatores, the fifth one being inserted in a membrane attached to the clavicle, and there is no trapezius in this fish. In Trigla and Scorpæna I also found (Allis, 1909) five external levatores, and I now find that there is no trapezius in either of these fishes. In Ameiurus there is a trapezius innervated by a branch of the vagus (Herrick, 1901, p. 209), and the levatores of this fish are none of them inserted on the fifth branchial arch (McMurrich, 1884). In Polypterus, Edgeworth (loc. cit., p. 241) finds a trapezius, and there are but four levatores in this fish.

These several facts regarding these fishes, when compared with Greil's descriptions of Ceratodus, seem certainly to warrant the conclusion that in the Teleostomi, as in Ceratodus, the trapezius is developed from the fifth branchial myotome, and that it always retains its normal and primitive innervation by the nerve of that segment of the body.

The musculi coracobranchiales are said by Dohrn to be developed, as already fully explained, from the deeper, proximal fibres of the ventral portions of the constrictores superficiales of the branchial arches and to be represented, in the adult, by those fibres as described by Vetter. They are accordingly said by Dohrn to be totally different muscles from the coracobranchiales of Vetter's descriptions of the adult, which are said by Dohrn to be simply the distal fibres of the ventral portions of the branchial constrictores superficiales, misnamed coracobranchiales by Vetter. Edgeworth says, as already explained, that the coracobranchiales are developed from the entire ventral ends of the branchial myotomes, and he considers the muscles so developed to be identical with the coracobranchiales of Vetter's descriptions of the adult.

The coracobranchialis of the first branchial arch of the

adult Heptanchus is said by Vetter to arise mainly from the tendinous dorsal surface of the musculus coracohyoideus; the coracobranchiales of the second to the fifth arches to arise mainly from the dorsal surface of the musculus coracoarcualis communis, but in part from a tendinous cord formed in the mid-ventral line of a fascia that covers, ventrally, the pericardial chamber; the sixth coracobranchialis to arise in part from the shoulder-girdle; and the seventh coracobranchialis to arise entirely from the shoulder-girdle. Running forward, these several muscles are all inserted mainly on the hypobranchial of the arch to which they are assigned, but certain of the fibres of the muscle of the first arch are inserted on the basihyal, and certain of the fibres of the muscles of the second to the sixth arches, and all of the fibres of the muscle to the seventh arch, on the ceratobranchial of the corresponding arch. Although not so stated by Vetter, the coracobranchiales must, because of these origins and insertions, in a measure embrace the pericardial chamber, running at first dorso-laterally and then dorso-mesially around it. Deeper (proximal) and distal fibres of the ventral portions of the constrictores superficiales both coexist with the several coracobranchiales.

In Acanthias and Scymnus the coracobranchiales, as described by Vetter, seem to differ from those in Heptanchus mainly in that they arise ventrally, in Acanthias, from the outer edge of the fascia that covers the pericardial chamber, and in Scymnus from the shoulder-girdle and a process of the fifth ceratobranchial. Marion (1905) says that, in Acanthias, the coracobranchialis is composed of five parts and forms the lateral wall of the pericardial chamber. In both Scyllium and Mustelus, as I have already fully described, musculi coracobranchiales coexist with both deeper (proximal) and distal fibres of the constrictores superficiales, and there is every reason to believe that similar conditions are found in both Acanthias and Scymnus.

In Chlamydoselachus I find the coracobranchiales of the third to the sixth branchial arches all arising, as a single

continuous muscle-sheet, from the lateral edges of a strong median fascia which is attached posteriorly, on either side, to the lateral edge of the ventral portion of the shoulder-girdle. This fascia extends anteriorly, beyond the united ventral ends of the shoulder-girdles, as a narrow median tendinous band, and, lying close against the ventral surface of the pericardial membrane, forms, with that membrane, the related ventral portion of the wall of the pericardial chamber. The fascia is apparently formed in large part by the tendons of origin of the fibres of the muscle-sheet, and from there the fibres run at first antero-dorso-laterally and then antero-dorso-mesially, thus encircling and enclosing the pericardial chamber and the truncus arteriosus. The musculi coracobranchiales of the third to the sixth branchial arches thus have every appearance of having been developed in intimate relations to the wall of the pericardial chamber, and of having retained their relations to that wall. The first and second coracobranchiales have become more or less independent of the pericardial wall and its related fascia. In this fish, as in Heptanchus, the deeper and distal portions of the ventral ends of the constrictores superficiales both coexist with the coracobranchiales.

The coracobranchiales of Chlamydoselachus are all innervated, as they are said by Vetter to be in the fishes examined by him, by a large nerve of spinal or spino-occipital origin, the exact origin and composition of which I have not as yet determined, this nerve also innervating the musculi coraco-arcualis communis, coracohyoideus, and coracomandibularis. This common innervation of these several muscles, their practical continuity in the adult Heptanchus, and the fact that, in Heptanchus, Chlamydoselachus, Scyllium, and Mustelus, coracobranchiales, innervated by spinal or spino-occipital nerves, coexist with both the deeper (proximal) and the distal fibres of the ventral portions of the constrictores superficiales, all of which latter muscles are innervated by branchial nerves, give every reason to believe that both Dohrn and Edgeworth have in some way misinterpreted the

muscles in embryos, and that the coracobranchiales of Vetter's descriptions are not each derived from the ventral end of the corresponding branchial myotome, as they are said to be by both those authors.

The coracobranchiales of these fishes must then either be developed from trunk myotomes, as the coracohyoideus and coracomandibularis are said to be; be developed, as in Ceratodus (Greil), from the ventral end of the axial mesoderm of the ultimate branchial arch, as will be later explained; or, possibly, be developed from some part of the cœlomic wall. Their innervation, as at present given, is decidedly against the supposition that they are developed from the myotome of the ultimate branchial arch, and in favour of their being developed from trunk myotomes, as the other hypobranchial muscles are said to be. The conditions in Chlamydoselachus, if this fish is as primitive a one as it is generally considered to be, would favour their being developed from the cœlomic wall, and this derivation has been ascribed to them, in other Selachii, by van Wijhe.

Van Wijhe says (1882 b, p. 16): "Der Musc. coraco-branchialis + coraco-mandibularis hat eine ganz andere Entstehungsweise als der coraco-hyoideus. Er entwickelt sich nämlich aus der unpaaren vorderen Verlängerung des Pericardiums, dessen Höhle, wie wir gesehen haben, im Stadium J mit den Höhlen der Visceralbogen communicirt. Nach dem Stadium K fängt diese vordere Verlängerung zu obliteriren an; die Zellen ihrer Wände werden Muskelfasern, und im Anfang des O ist die ganze Höhle geschwunden; ihre muskelösen Wände sind zusammengekommen, und bilden die Anlage des Musc. coraco-mandibularis + coraco-branchialis. In späten Stadien ist derselbe immer leicht von dem Musc. coraco-hyoideus zu unterscheiden. Die Nebenzweige, welche ersterer zu den Visceralbogen abgeibt, sind aus den Unterenden der Wände der Visceralbogenhöhlen entstanden."

The "Nebenzweige" above referred to by van Wijhe are quite certainly simply the deeper, proximal fibres of the ventral portions of the constrictores superficiales, which

coexist, in Heptanchus, Scyllium, and Mustelus, with the coracobranchiales and are inserted on them, but form no part of them. The coracobranchiales would then not be derived in any part from branchial myotomes, and their primitive innervation would depend upon what nerve or nerves innervated the parts of the pericardial wall from which they were derived, and this might evidently be either by branchial or postbranchial nerves. But if these muscles and the coracomandibularis are both derived from cells of similar origin, as van Wijhe states, and if the coracomandibularis was primarily innervated by spinal or spino-occipital nerves, the coracobranchiales must certainly also have been so innervated, and even Edgeworth does not question that the coracomandibularis was primarily as well as actually innervated by those nerves. Edgeworth furthermore says (loc. cit., p. 178) that no muscles are directly formed from the walls of the branchial portion of the cephalic cœlom, which, if correct, would indicate that the muscles described by van Wijhe were developed in the postbranchial, or spinal, region. The anatomical evidence is also all strongly in favour of the similarity of origin of these muscles ascribed to them by van Wijhe, and until the conflicting embryological evidence has been controlled it accordingly seems proper to conclude that all the so-called hypobranchial muscles are of similar origin, and that they were primarily, as they are actually, innervated by spinal or spino-occipital nerves.

In Chimæra coracobranchiales are said by Vetter (1878) to be found, and to there closely resemble the muscles found in the Selachii. These muscles are thus found in all the Elasmobranchii, and in all of these fishes they are said to be innervated by spinal or spino-occipital nerves.

In the Teleostomi and Dipneusti, coracobranchiales have been described as such in certain fishes, while, in other fishes, muscles described under other names are said to be the homologues of the coracobranchiales of the Elasmobranchii.

In Acipenser the coracobranchiales of the first three

branchial arches are said by Vetter (1878) to be represented by special tendons of the musculus coracoarcualis anterior which are inserted, one each, on the hypobranchial of the corresponding arch, the main tendon of the muscle being inserted on the hypohyal. The coracobranchialis of the fourth arch is said to be probably wanting. The coracobranchialis of the fifth arch is said to be represented by the single tendon of the coracoarcualis posterior, which tendon is inserted on a ligament which extends from the basibranchial of the fourth arch to the ventral end of the rudimentary branchial bar of the fifth arch. Fürbringer (1897, p. 460) found the tendon of the latter muscle separated into two parts, one of which was inserted on the branchial bar of the fourth arch and the other on that bar of the fifth arch. Vetter says that all these muscles are innervated by spinal nerves.

The coracobranchiales of the adult Acipenser are thus said to be so completely fused with the coracoarcuales anterior and posterior that they appear as simple tendons of those muscles, and Edgeworth says (loc. cit., p. 235) that these tendons are developed from downgrowths of the lower ends of the first, second, third, and fifth branchial myotomes, while the coracohyoideus, which is Vetter's coracoarcualis anterior together with the tendon inserted on the hypohyal, is said (loc. cit., p. 268) to be of spinal origin. No downgrowth, giving rise to a coracobranchialis, takes place in the fourth arch, this arch thus forming, for some inexplicable reason, a marked exception to the other arches.

This interpretation of these several muscles of Acipenser, based by Vetter on anatomical and by Edgeworth on embryological investigations and considerations, may perhaps be the correct one, but I strongly doubt it. Comparing the conditions in this fish with those in Heptanchus, Scyllium, and, Mustelus, as I have described them, it seems much more probable that the so-called coracobranchiales of the first three branchial arches of Acipenser are simply the homologues of the proximal fibres of the ventral ends of the con-

strictores superficiales of Heptanchus, Scyllium, and Mustelus, and not the homologues of the hypobranchial coracobranchiales of those fishes. The musculus coracoarcualis posterior of Acipenser, if its innervation by spinal nerves is correct, might be the homologue of the coracobranchiales of the Selachii, but this innervation needs confirmation.

In Ceratodus, coracobranchiales are said by Edgeworth to be developed from the ventral ends of the second, third, and fifth branchial myotomes, but not from those ends of the first and fourth myotomes. In later stages, still another coracobranchialis is said to be differentiated from the already differentiated interarcualis ventralis of the first branchial arch. Greil gives quite a different account of the origin of these muscles. According to him (1913) there is but one coracobranchialis on either side of the head of this fish, and it is said, as already explained, to be developed from the external one of two processes of the ventral end of the axial mesoderm of the fifth branchial arch, that mesoderm being derived from a ventral process of the second trunk myotome. The muscle is said by Greil (loc. cit., p. 1344) to grow forward and separate into three or four heads which acquire insertions on the ventral ends of the branchial bars. The ventral ends of the axial mesoderms of the first to the fourth branchial arches are said to develop, respectively, into the musculi ceratohyoideus, interbranchialis anterior, interbranchialis posterior, and interbranchialis IV, while from the deeper one of the two processes from the ventral end of the axial mesoderm of the fifth arch the dorsopharyngeus is said to be developed; all of these muscles being said to be serial homologues one of the other and all wholly independent of the coracobranchialis.

In Amia, Edgeworth says (loc. cit., p. 237) that only one coracobranchialis is developed, the coracobranchialis V, and this muscle, in 14 mm. embryos, is said to divide into the pharyngoclaviculares externus and internus of the adult. In the Teleostei the development of these muscles is not particularly described, but references made by Edgeworth to

those fishes make it certain that the conditions were there considered by him to be similar to those in Amia. In Polypterus senegalus the musculi pharyngoclaviculares are said to be developed as in Amia, but from the ventral end of the fourth instead of the fifth myotome.

Regarding the innervation of the coracobranchiales, Edgeworth says (loc. cit., p. 253): "A coraco-branchialis, or pharyngoclavicularis externus and internus, developed by backward growth from the last branchial myotome, i. e. fourth in Polypterus senegalus, fifth in Amia, Salmo, Menidia, may either retain its original branchial innervation from the tenth, e.g. Amia (Allis), Esox (Vetter), Menidia (Herrick), Lepidosteus, Polypterus senegalus, or be innervated by spino-occipital nerves, e.g. Amiurus (Wright), Salmo (Harrison). When coraco-branchiales are developed from all the branchial myotomes, they are innervated by the spino-occipital nerves, e.g. Selachii (Vetter, Fürbringer), Acipenser (Vetter), Polypterus ? species (Fürbringer), Ceratodus (Fürbringer)."

Certain of the musculi coracobranchiales are thus, like the trapezius, muscles said by Edgeworth to be innervated by the nerve of a segment of the body other than that from which the muscle is derived. The muscles said by him to be innervated by the nervus vagus can be left out of account in this respect, and the muscles in the Selachii, and the tendons that are said to represent the muscles in Acipenser, have been already considered. In Ceratodus, the dorsocleidobranchialis of Greil's (1913) descriptions, from which the so-called coracobranchialis is said to be developed, is said by that author to be innervated, in embryos, by the nervus vagus, and although Fürbringer (1897), who is quoted by Edgeworth, includes this muscle of this fish in the hypocranial spinal muscles, innervated by spino-occipital nerves, I cannot find that he himself traced their innervation by branches of those nerves. In Ameiurus, Herrick (1901, p. 209) says that the pharyngoclaviculares are innervated by the vagus, and not by spinal nerves as they were said to be by Wright, and I have con-

trolled and confirmed this innervation by the vagus in sections that I have of this fish. In sections of a 75 mm. specimen of Polypterus senegalus I also find these muscles innervated by a branch of the vagus and not by spino-occipital nerves. In Polyodon, which is not cited by Edgeworth, the pharyngoclaviculares are said by Danforth (1913) to be practically continuous, at their origin from the shoulder-girdle, with the coracoarcualis, and to be innervated, as the latter muscle is, by spinal nerves; and Danforth adds: "I could trace no branches of the vagus into their upper ends." I however find, in a series of transverse sections of a 141 mm. specimen of this fish, a branch of the vagus going into the upper ends of these muscles and apparently innervating them. The large spinal nerve that innervates the hypobranchial muscles passes close to the ventral ends of the pharyngoclaviculares, but no branch could be found entering them. An artery that accompanies the large spinal nerve leaves it and enters the pharyngoclaviculares.

The anatomical evidence regarding these muscles in the Teleostomi and Dipneusti is thus, as in the case of the Elasmobranchii, against the view that they have undergone a secondary change of innervation, but it is strongly in favour of the view that there are, in these several fishes, two totally different sets of muscles that have both been called coracobranchiales, one being of spinal or spino-occipital and the other of branchial origin. The muscles of spinal or spino-occipital origin are found in the Elasmobranchii, while those of branchial origin are found in the Teleostomi and Dipneusti. In the Teleostomi, with the possible exception of Polypterus (Edgeworth), the muscles are derived from the ventral half of the primitive constrictor superficialis of the ultimate branchial arch, this portion of this constrictor thus being utilised, in these fishes, for the secondary purpose of forming this muscle just as the dorsal portion of this muscle has been utilised, in the Elasmobranchii, for the secondary purpose of forming the musculus trapezius. In the Elasmobranchii the muscles are quite probably derived either from trunk myotomes or from the

walls of the cœlomic cavity, and hence not from branchial myotomes.

The development of these muscles in Ceratodus, as described by Greil, may perhaps offer an explanation of this difference of innervation and apparent derivation of these muscles in these two large groups of fishes. The coracobranchiales of Ceratodus are said by that author to be developed from a ventral process of the posterior half of the second trunk myotome. From a similar ventral process of the entire third trunk myotome a large muscle is said to be developed (1913, p. 1140) which acquires insertion on the hypohyal and ceratohyal and hence is evidently a musculus coracohyoideus, and from this muscle the coracomandibularis is differentiated. Similar ventral processes of the fourth and fifth trunk myotomes form the posterior portion of the hypobranchial muscles, these portions evidently representing the musculus coracoarcualis of the Selachii; and these muscles are all innervated by branches of a nerve formed by the fusion of the nerves of the fourth and fifth trunk segments (myotomes). Of these nerves Greil says (loc. cit., p. 1139): "Es besteht jedoch keine engere Zugehörigkeit zu den betreffenden Segmenten, jeder Nerv versorgt auch den Myotomfortsatz des vorderen Segmentes, was sich schon daraus ergiebt, dass der dritte Segmentalnerv in der Regel keinen ventralen Nerven an die hypobranchiale Musculatur abgiebt." Here it is said that the coracobranchiales and the coracomandibularis + coracohyoideus are derived from ventral processes of adjoining segments of the trunk which differ only in that one of them becomes affiliated with the branchial arches and acquires innervation by the vagus, while the other retains its affiliation with the trunk myotomes and acquires innervation by the nerve of the next posterior trunk segment. This change of innervation, based on embryological evidence alone, I am always inclined to doubt, but it is to be noted that if the process of the second trunk myotome had retained its primitive relations to the other trunk myotomes, instead of undergoing some sort of change because of its

affiliation with the branchial myotomes, the coracobranchiales would have been innervated by a spino-occipital instead of by a branchial nerve ; and this is possibly what has occurred in the Selachii.

An adductor arcus branchialis is said by Vetter to be found, in all the Selachii examined by him, in each of the fully developed branchial arches, which would seem to exclude the ultimate arch in each of these fishes, that arch certainly not being fully developed. In Chimaera, Vetter says that similar muscles are found in the first three branchial arches, but that the corresponding muscles in the fourth and fifth arches resemble the arcuales dorsales of the Selachii rather than the adductores of those fishes. Tiesing (1895) says that in Mustelus and the Batoidei there is an adductor muscle in each arch, and I find an adductor in each of the six arches of the one specimen of Chlamydoselachus that I have examined for this purpose. Fürbringer (1903, p. 397) did not find an adductor in the first branchial arch of his specimen of Chlamydoselachus. Vetter says that the adductores in the Selachii, and also in Chimaera, are all innervated by branches of the nervus vagus of the related arch, but he does not give the course of those branches. Tiesing gives the same innervation in the Selachii and Batoidei examined by him, and he adds that the branch of the vagus that innervates the muscle perforates, in each case, the related epibranchial in order to reach the muscle. In Chlamydoselachus I also find the nerve perforating the related epibranchial, near its anterior edge. The muscle, in all the Plagiostomi, and in the first three branchial arches of Chimaera, arises from the internal surface of the epibranchial of its arch and is inserted on the opposing, internal surface of the ceratobranchial of the arch.

In the Teleostei, Vetter (1878) found no adductores arcuum branchialium excepting in one large specimen of Esox, in which specimen they are said to be represented by a few scattered muscle fibres lying in connective tissue in the angle

between the epibranchial and ceratobranchial in each of the first three branchial arches. These fibres being found only in a particularly large specimen of this fish, does not favour the view that they are persisting fibres of a muscle that is in process of reduction; for one would naturally expect to find such a muscle relatively the more developed the younger the fish. In Ameiurus, Wright (1885) did not find any of these muscles, and they are said by Pollard (1892) not to be found in Polypterus. In the Dipneusti, also, they are apparently not found, for Fürbringer (1904) makes no mention of them in his descriptions of those fishes.

In Amia, I described (Allis, 1897) two adductores arcuum branchialium, one related to the fourth and the other to the fifth branchial arch. The fourth adductor arises from the internal surface of a posteriorly projecting process of the fourth epibranchial, and is inserted on a similar process of the fourth ceratobranchial, the muscle thus lying on the posterior surface of the branchial bar. The fifth adductor extends from the opposite side of the process of the fourth ceratobranchial just above mentioned to the fifth ceratobranchial, lies somewhat on the posterior surfaces of those two cartilages, and is in part continuous, ventrally, with the transversus ventralis posterior. The branch of the vagus that innervates these muscles passes, in each case, over the posterior edge of the related branchial bar.

In Polyodon, Danforth (1913) finds an adductor arcus branchialis in each of the first four branchial arches. Each muscle arises from the flat posterior surface of the related epibranchial, the surface of origin not approaching the margin of the cartilage at any point, and the muscle is covered by a tough aponeurotic sheet which binds it to the cartilage and also serves as a secondary basis of origin. Running ventro-laterally each muscle passes between the epibranchial and ceratobranchial of its arch and is inserted on the anterior surface of the latter cartilage. Branches of the nervus vagus of the related arch are sent to the muscle, passing, in each case, over the posterior edge of the related epibranchial.

Fibres of the ramus post-trematicus internus of the next posterior arch are said to also enter the muscle, but Danforth could not determine whether they were motor or sensory nerves.

In Acipenser, Vetter (1878) found a small adductor in each of the first three branchial arches.

Adductores arcuum branchialium are accordingly described only in the Elasmobranchii and Ganoidei, and in these two groups of fishes there is marked difference, not only in the position of these muscles, but also in their manner of innervation. The muscles in these two groups of fishes cannot, then, be homologous if the innervation of muscles, and the relations of nerves to skeletal structures, are as constant as I consider them to be. That the nerves that innervate the muscles in Amia and Polyodon have cut through the related epibranchials, from their anterior to their posterior surfaces, the perforation of the cartilage in the Plagiostomi representing an intermediate stage in this process, I, on principle, greatly doubt, and, furthermore, Dohrn's observations offer a different and more probable explanation of the conditions in the latter fishes. According to that author (1884, p. 111), a concentration of mesoderm cells takes place, at a certain stage in embryos of these fishes, posterior to the proximal edge of the related myotome, and soon afterwards a second concentration of similar cells takes place anterior to the myotome. These two groups of cells are said to represent the beginnings of the chondrification of the branchial bar of the arch, but it is not said how or when the two groups fuse. That part of the myotome of the arch that lies between the two groups of cells is said to later differentiate as the adductor of the arch, and it would seem as if the nerve that innervates the muscle so differentiated would of necessity lie between the two groups of cells, and hence later perforate the branchial bar, and this seems to find confirmation in conditions that I find in my 42 cm. specimen of Scyllium. In this fish each musculus adductor has its insertion, at either end, in a pit in the related epibranchial or ceratobranchial, and in each of the ceratobranchials this pit

in part perforates the cartilage, the muscle strands of the adductor there being directly continuous with those of the musculus interbranchialis of the arch. The adductor is thus here not yet fully cut off from the primitive constrictor of its arch, and if the epibranchial were similarly perforated in younger stages it is certain that these particular strands would be innervated by a nerve that traversed the perforation of that cartilage.

If this be the explanation of the conditions in the Plagiostomi, it is quite certain that the conditions in the Ganoidei were not derived from them. The conditions in these latter fishes are associated with, and quite undoubtedly correlated to, the presence of the straight form of branchial bar instead of the sigma form, and to the absence of cartilaginous branchial rays. Where these latter rays are found, the constrictor muscle of an arch could slip, or project, over the anterior edge of the related branchial bar, as described by Dohrn in plagiostoman embryos, and so give rise to an adductor muscle, but it could not so slip over the posterior edge of the bar. The ganoidean adductores could not, accordingly, have been developed in a fish already possessed of cartilaginous branchial rays, and it would even seem as if they could not have been developed in a fish already possessed of the cartilaginous or osseous rods that support the branchial filaments in all the Teleostomi. These osseous rods I have already described in Scomber (Allis, 1903), and I now find similar supporting rods, of cartilage instead of bone, in Amia, Polyodon, and Polypterus. In Amia they are not evident until the fish is over 12 mm. in length. These rods are found in two series, one along the anterior and the other along the posterior edge of the branchial bar, and it would seem as if a constrictor muscle, which must primarily have occupied a position between their lines of attachment to the branchial bar, could not, after their development, have slipped over either edge of the bar. The Ganoidean adductores must accordingly have been differentiated before these supporting rods were developed. In a specimen of Ceratodus

that has been long and not well preserved in alcohol, I do not find any of these supporting rods, and descriptions of this fish do not speak of them. There are also no adductores arcuum branchialium in this fish, but there are persisting remnants of the constrictores superficiales, as already explained. In such a fish as this, certain of the fibres of the constrictor of an arch might slip over onto the posterior surface of its arch and so give rise to the ganoidean adductor.

One other branchial muscle may here be mentioned, the retractor arcuum branchialium, found in Amia, Lepidosteus, and certain of the Teleostei, for this muscle is said by Edgeworth to be developed from trunk myotomes and to later acquire an innervation by a branch of the vagus. I have, however, recently shown (Allis, 1915) that this muscle of the Teleostei is quite certainly the homologue of a muscle, found in Chlamydoselachus, which is simply a differentiation of the anterior end of the constrictor œsophagi. If I am right in this conclusion, the innervation of the muscle of the Teleostei is normal and primary, and not secondary.

From the embryological and anatomical facts above presented regarding the several muscles related to the branchial arches, it seems quite certain that, in the gnathostome fishes, the primitive condition of these muscles was, as Vetter long ago concluded, a simple annular constrictor in each arch ; and, to act as such a constrictor of the enclosed cavity, the muscle must have been attached both dorsally and ventrally either to some fixed structure or to its fellow of the opposite side. If attached primarily, at either end, to the related branchial bar, the muscle could not have acted as a constrictor.

The branchial bar, in this primitive condition, probably lay directly internal to the constrictor muscle, Dohrn's assertion that it lies posterior to the proximal edge of the myotome from which the muscle is developed probably applying only to early stages in the Elasmobranchii. The muscle and its related branchial bar probably lay primarily

in a plane perpendicular to the axis of the body, but this plane later became inclined to that axis, the acute angle lying posterior to the plane; and still later it acquired, in the Elasmobranchii, the well known sigma form. What impressed this sigma form on these arches is not known, but it would seem as if it must have been related to the relative lengths of the pharyngeal cavity and the occipital portion of the chondrocranium. But, whatever the cause, this sigma form of arch has definitely associated with it, in recent fishes, the presence of cartilaginous branchial rays, of musculi constrictores superficiales, and of musculi adductores arcuum branchialium of the plagiostoman type; while associated with the other, or straight, form of arch is the absence of the above cited features, the presence of supporting rods in the branchial filaments and of musculi levatores arcuum branchialium, and the occasional presence of musculi adductores arcuum branchialium that are innervated by nerves that pass over the posterior edge of the branchial bar of the related arch.

In Ceratodus, it is probable (Allis, 1915) that there are much reduced pharyngobranchials and that they are directed postero-mesially, as they are in the Elasmobranchii, while the hypobranchials are directed antero-mesially, as in the Teleostomi; and in this fish there are no adductores and apparently no supporting rods to the branchial filaments, but there are so-called musculi interbranchiales which are probably persisting remnants of the plagiostoman constrictores superficiales.

This limitation of cartilaginous branchial rays or supporting rods in the branchial filaments, together with certain other associated and distinctive features, to the Elasmobranchii and Teleostomi respectively, and the probable absence of both branchial rays and supporting rods in Ceratodus, would seem to favour the view that the Teleostomi were descended from a fish in which the cartilaginous branchial rays had not yet been acquired. I have, however, quite recently (Allis, 1915) concluded that the basal portions, at least, of the cartilaginous extrabranchials are archaic structures, and that they are found, in modified form, either in the

branchial arches, in the hyal and mandibular arches, or fused with the neurocranium, not only in all living Teleostomi but also in most, if not all, higher vertebrates. If this conclusion is correct, and if these extrabranchials are simply modified branchial rays, as is generally accepted, then the early ancestors of the Teleostomi must have possessed those rays. But I have, since the publication of the paper above referred to, found that Braus (1906) concludes, from conditions found in embryos of Heptanchus, that the extrabranchials belong to an independent category of skeletal pieces. If this be so, it then seems probable that the early ancestors of the Teleostomi possessed these particular cartilages, but not the ordinary branchial rays with which they are usually associated.

The branchial muscles of the Selachii seem to be more primitive than those of any other of the gnathostome fishes. When, in the ancestor of the Selachii, the branchial arches acquired positions oblique to the axis of the body, and later, or at the same time, acquired the sigma form, the proximal edge of the simple dorso-ventral constrictor of each arch slipped, in the middle of its length, over the anterior (actually lateral) surface of the branchial bar of its arch, and the fibres of the muscle, where they crossed the branchial bar, there first became tendinous, by the interruption of their muscular substance, and were then later cut through by acquiring insertion on the bar. A triangular piece was thus cut out of the proximal edge of the muscle, and became the adductor of the arch. The gill-pouch anterior to the arch, pressing against the anterior surface of that part of the constrictor that remained external to the branchial bar, first caused a simple thinning of the muscle. The dorsal and ventral rays of the branchial series were then modified, as extrabranchials, in supporting relations to this thinned part of the muscle, or these extrabranchials were otherwise and independently developed for the same purpose, and at certain places in the lines where the muscle passed over these cartilages, it again became tendinous, or acquired insertion on the cartilages.

Two narrow and more or less extensive incisures were thus made in the muscle, and that part of the muscle that lay between these two incisures became the musculus interbranchialis. Where the muscle fibres were not thus cut through, or did not become tendinous, the musculus interbranchialis was simply a thinner portion of the primitive and continuous constrictor. That portion of the muscle that lay distal to the extrabranchials remained intact, and formed the continuous dorso-ventral fibres of the constrictor superficialis. The dorsal and ventral ends of the constrictores had, in the meantime, and in certain fishes, turned posteriorly, possibly influenced by the sigma form of the branchial bars. The arcual and interarcual muscles were then differentiated, and this, together with the overlappings and fusions of the dorsal and ventral portions of the constrictores superficiales with each other and with the musculus trapezius, and the formation of tendinous aponeuroses where the muscle fibres crossed the underlying extrabranchials, produced the many variations found in the adult. The constrictor of the ultimate branchial arch was utilised to form the musculus trapezius.

In the Teleostomi, the straight form of arch was retained, and correlated to this the constrictores superficiales did not slip over the anterior edges of the related arches, but, in certain fishes, certain of them slipped over the posterior edge of the related arch and gave rise to the ganoidean adductors. The constrictor of each branchial arch then apparently became rudimentary in the middle of its length, doubtless because of modifications in the branchial lamellæ and the development of supporting branchial rods, but it was in part utilised to form the delicate radial muscles related to the supporting branchial rods. The dorsal and ventral portions of the primitive constrictor then became the levatores, and the transversi and obliqui dorsales and ventrales, and the ventral portion of the constrictor of the ultimate arch became the coracobranchiales, or their homologues the pharyngoclaviculares. The levator of the ultimate branchial arch became, in certain of these fishes, a musculus trapezius.

Edgeworth comes to totally different conclusions regarding the primitive condition and the later differentiations of these muscles. He says (l. c. p. 259): "The probable primitive condition of each of the branchial myotomes was, from above downwards, a levator, a marginalis, an interarcualis ventralis, and (the lateral half of) a tranversus ventralis," which would seem to imply that there was, in this primitive condition as conceived by him, no simple continuous constrictor extending the full length of the arch. The interarcuales ventrales are said by him to be muscles that extend between the ventral ends of the branchial bars. The marginales are said (l. c. p. 233) to be muscles found by Schultze in anuran larvæ and having their exact homologues in what Edgeworth calls the vertical muscles of Ceratodus. These vertical muscles of Ceratodus are called by both Fürbringer (1904) and Greil (1913) the interbranchiales, and they are said by Fürbringer to extend from the neurocranium to a process on the ventral end of the ceratobranchial of the arch next anterior to the one to which the interbranchialis belongs. It would accordingly seem as if these muscles must be remnants of the primitive constrictor of the arch and not interbranchiales; and yet Edgeworth intercalates them, in each branchial arch of the primitive vertebrate, between the musculi levator and interarcualis ventralis of that arch. Edgeworth (l. c. p. 178) considers the branchial muscles in the Amphibia to represent the most primitive condition found in any vertebrate, and he (l. c. p. 176) furthermore thinks it probable that there were, in the primitive vertebrate, but two branchial arches, and that where other arches are now found they have been subsequently added posterior to those two.

Hyal Arch.

Dohrn (1885) says that, in the hyal arch of selachians (Plagiostomi), that proximal portion of the myotome (Musculatur) out of which, in the branchial arches, the adductor is developed is wanting, its formation having been wholly pre-

vented by the one commissure formed, in this arch, in relation to the efferent arteries. The musculi interarcuales are also wanting in this arch, but it is said that in their place there is a complicated system of ligaments. It is not said that these ligaments are developed from any part of the myotome of the arch, but this would seem to be implied, the ligaments then representing the missing musculi interarcuales. In the ventral part of the arch the muscles are said to be found, undiminished in number, exactly as in the branchial arches.

The distal portion of the myotome (Musculatur) is said to form the constrictor superficialis of the arch, which is richly developed, especially in its ventral portion. Dorsally this constrictor is said to turn posteriorly and fuse with the corresponding portion of the muscle of the first branchial arch. Ventrally, the distal portion of the constrictor is said to fuse with a similarly named portion of a myotome (Muskelschlauches) which comes from the mandibular arch, the two muscles, together, then running ventrally and fusing with the fibres of the coracohyoideus and coracomandibularis exactly as the "other coracobranchiales" do (in der Weise der ürbigen M. coraco-branchiales). This expression evidently affirms that the distal portions of the ventral ends of the constrictores superficiales of the hyal and mandibular arches represent the coracobranchiales of those arches, and it would seem to imply that the coracobranchiales of the branchial arches were derived from the corresponding portions of the constrictores superficiales of their arches. But as, as has already been fully explained, the coracobranchiales of Dohrn's descriptions are said by him to be developed from the proximal portions of the myotomes of their respective arches, it must be that the coracobranchiales here referred to are the muscles so named by Vetter, but said by Dohrn to have been wrongly identified by him. What becomes of the remaining, proximal fibres of the ventral portion of the hyal myotome is not said, notwithstanding that they have been said to exist exactly as in the branchial arches. The descriptions are thus not clear, but it is important to note

that the ventral end of the constrictor of the hyal arch fuses with a muscle developed from a corresponding portion of the mandibular myotome.

Edgeworth says (1911, p. 206) that in 14 mm. embryos of Scyllium, the ventral end of the hyal myotome becomes continuous with the lateral edge (morphologically the dorsal end) of the future interhyoideus, this latter muscle being said to be developed, as will be later explained, from the walls of the cœlomic cavity and not from the hyal myotome. In 16 mm. embryos the myotome is said to be partly continuous with the interhyoideus and partly inserted on the lateral surface of the hyal bar to form a levator hyomandibularis (levator hyoidei, Edgeworth). In later stages the myotome becomes separated from the interhyoideus, and the lateral edge (dorsal end) of the latter muscle is inserted on the ceratohyal. A backward extension of the myotome and the interhyoideus then takes place, and a continuous dorso-ventral muscle-sheet is thus formed, which lies posterior to the hyal bar, and is said to be the muscle C_2vd of Ruge's (1897) descriptions of the adult. This dorso-ventral sheet is accordingly said to be formed, in its dorsal portion, by fibres derived from the hyal myotome, and in its ventral portion by fibres derived from the cœlomic wall. The constrictor superficialis of the hyal arch is accordingly not the strict serial homologue of the constrictores of the branchial arches, although this is not so stated by Edgeworth. It is said that the primary form of the interhyoideus, developed from the cœlomic wall, would appear to have been a transverse band connecting the two hyal bars.

In the adult Selachii the muscles of this arch have been described by Vetter, Tiesing, Ruge, and Marion, Ruge's descriptions being particularly complete. In this arch no musculi interbranchialis, arcualis, or interarcualis are differentiated; but, according to Dohrn, the two latter muscles may be represented by ligaments. A musculus interbasalis (Interarcualis dorsalis I, Vetter) may be found extending from this arch to the first branchial arch (Allis, 1915), but

this muscle is derived from trunk myotomes and not from branchial ones.

In Heptanchus (Vetter), Hexanchus (Ruge), and Chlamydoselachus the fibres of the constrictor superficialis of the hyal arch have a nearly dorso-ventral course, but in most other Selachii that have been described the dorsal and ventral ends of this constrictor are directed more or less posteriorly, and it is probable that in all these latter fishes, as is certainly the case in my specimen of Mustelus, the distal (posterior) fibres cross, in their course, the extrabranchials of one or more of the branchial arches. In certain of these fishes the ventral fibres extend posteriorly nearly or quite to the ventral end of the shoulder-girdle. The fibres of the muscle may become tendinous where they cross the extrabranchials of the branchial arches, particularly the dorsal extrabranchials. They do not usually become tendinous where they cross the extrabranchials of their own arch, nor are they inserted on those extrabranchials, this doubtless being due to the absence of an overlapping branchial diaphragm and gill-pouch, and accounting for the absence of a musculus interbranchialis in this arch. In the middle of the length of the constrictor, opposite the hyomandibulo-ceratohyal articulation, the muscle fibres are, probably in all Selachii, interrupted by a more or less extensive aponeurosis. Dohrn describes this aponeurosis even in embryos, but it is evident that the fibres must here have been primarily continuous, and Ruge (1897, p. 224) says that the conditions in the adult Hexanchus warrant this conclusion.

In the proximal edge of the constrictor there is, as in the branchial arches, a large angular incisure, and this incisure is filled by the articulating ends of the epihyal and ceratohyal, the cut ends of the fibres being inserted on those cartilages. Comparison with the conditions in the branchial arches would then seem to make it practically certain that a piece has here been cut out of this hyal muscle, as it has been cut out of the branchial muscles, and that the pieces so cut out of these several muscles were all serial homologues. If this be so,

some indication of the piece so cut out of the hyal muscle should be found in some stage of development of these fishes. According to Dohrn, it is not found in embryos, and he further says that the conditions there are such as to preclude the possibility of its development. There is, however, in the adults of these fishes a large and important ligament, the inferior postspiracular ligament, found in the hyal arch but not in the branchial arches, and not accounted for in Dohrn's descriptions of embryos.

In a recent work I suggested (Allis, 1915) that this inferior postspiracular ligament of the Selachii was probably derived from the musculus arcualis dorsalis of the hyal arch. I at that time accepted the currently expressed opinion that an adductor muscle was not differentiated in this arch, or that if differentiated it had later completely aborted. My present work leads me to doubt both these assumptions, and it now seems to me much more probable that the ligament is derived from the adductor of the arch than from the arcualis dorsalis. The ligament is found in nearly all, if not in all, the Selachii, and it is not found either in the Batoidei or the Teleostomi. In the Teleostomi the plagiostoman adductores are not found even in the branchial arches, as has been already fully explained, this accounting for the absence of the ligament in the hyal arch of these fishes; and the reason for its absence in the Batoidei will be considered immediately below. In the Selachii, the adductor, probably developed exactly as in the branchial arches, ceased to be of functional value, doubtless because of the intimate attachment of the cartilages of the arch to those of the mandibular arch, and, travelling upward along the epihyal until it reached and acquired insertion on the chondrocranium, it became the inferior postspiracular ligament. The relations of the ligament to the nerves, arteries, and veins of the region, said by me to be in accord with the derivation of the ligament from the arcualis dorsalis of the arch, are equally in accord with its derivation from the adductor of the arch, and, while the ligament might apparently have been developed from either muscle, the derivation

from the adductor is much more in accord with the conditions in the Batoidei.

In the Batoidei there is no inferior postspiracular ligament. In these fishes the proximal portion of the myotome of the hyal arch apparently passed over onto the anterior surface of the cartilaginous bar of the arch exactly as in the branchial arches, but, because of the marked change in the angle between the epihyal and ceratohyal (see Parker, 1876, Pl. 61, fig. 4), and the separation of the epihyal from the pharyngohyal, which latter element was utilised to form the hyomandibula (Allis, 1915), the proximal portion of the myotome here separated from the distal portion throughout its entire length, and no small middle portion was cut out to form an adductor. The proximal portion then acquired attachment on the pharyngohyal (hyomandibula) and gave rise to the musculi levator and depressor hyomandibularis of Tiesing's (1895) descriptions, and possibly also to the depressor mandibularis, which is said by Tiesing to be innervated by the nervus facialis. The remaining, distal portion of the myotome formed the constrictor superficialis. No adductor muscle being differentiated in this arch in these fishes, an inferior postspiracular ligament was naturally never developed.

Ruge says that, in the Selachii, the dorsal and ventral portions of the hyal constrictor superficialis both tend to separate into superficial and deeper layers, the former acquiring an insertion on the mandibular cartilages while the latter retains its primary insertion on the hyal cartilages. The insertion of certain of the fibres on the mandibular cartilages he considers to be an ancient acquisition of these fishes, and whenever it is wanting, in recent fishes, he considers it to be due to retrogression. The nervus hyoideomandibularis facialis is said to always lie external (anterior) to that part of the hyal constrictor that is inserted on the hyal cartilages, and to usually, but not always, lie internal (posterior) to the fibres inserted on the mandibular cartilages. In the region of the hyomandibulo-ceratohyal articulation,

where the constrictor never separates into superficial and deeper layers, the nerve apparently always lies on the external (anterior) surface of the muscle.

In the several figures given by Ruge, the nervus facialis is seen to lie internal to the dorsal portion of the hyal constrictor superficialis only in Heptanchus and possibly, in part, in Spinax; the nerve in the latter fish first lying on the external surface of the muscle and then apparently piercing it before it, the nerve, reaches the level of the hyomandibulo-ceratohyal articulation. In all of the many excellent figures of these fishes given by Luther (1909), the nerve lies internal to this part of the constrictor only in Heptanchus, Hexanchus, and Lamna. In the remnant of a head of Lamna that I have, I find the anterior fibres of the proximal portion of this part of the constrictor inserted on the palatoquadrate, but the remaining proximal fibres inserted on the hyomandibula. The nervus facialis lies internal to those fibres that are inserted on the palatoquadrate, but, beyond those fibres, it lies between the palatoquadrate and the hyomandibula, and hence external to the fibres inserted on the latter cartilage. In all the other Selachii figured by both Ruge and Luther, the nervus facialis lies external to all the fibres of this portion of the hyal constrictor.

In Heptanchus and Hexanchus the hyomandibula is relatively slender and lies internal to the palatoquadrate (Gegenbaur, 1872). In Lamna I find the dorsal end of the hyomandibula lying internal to the palatoquadrate. In all the other Selachii figured by Ruge and Luther, the dorsal end of the hyomandibula, so far as I can determine from existing descriptions at my disposal, lies posterior to the palatoquadrate and separated from it by a considerable interval, as shown in Gegenbaur's figures of Mustelus, Scymnus, Centrophorus, and Heterodontus. This, then, probably gives an explanation of the differing relations of the nervus facialis to the dorsal portion of the hyal constrictor. Where the dorsal end of the hyomandibula lies internal and close to the palatoquadrate, the nervus facialis also lies internal and close to the

latter cartilage. The fibres of the hyal constrictor, all primarily inserted on the hyomandibula, were then overlapped externally by the palatoquadrate, and the dorso-posterior edge of the latter cartilage lay posterior (distal) to the nervus facialis. The superficial fibres of the hyal constrictor then acquired insertion on the palatoquadrate along the line where the dorso-posterior edge of that cartilage crossed them, and so acquired a position external to the nervus facialis. Other, deeper fibres of the muscle then followed and joined the superficial ones. Where the dorsal end of the hyomandibula lay at a considerable distance from the palatoquadrate, the fibres of the constrictor simply pushed bodily forward, carrying the nervus facialis with them, and so retained their primitive position internal (posterior) to that nerve.

In the Holostei and Teleostei the conditions are here quite different from those in the Selachii. In the former fishes, the epihyal does not acquire articulation with the neurocranium; the posterior articular head of the hyomandibula quite certainly being formed by the fusion of the suprapharyngobranchial of the arch, derived from the basal portion of the extrabranchial of the arch, with the epihyal (Allis, 1915). That part of the constrictor superficialis that lay dorsal to the suprapharyngobranchial (extrabranchial) must then have been cut off from the ventral portion of the constrictor, and, lying between the suprapharyngobranchial and the cranial wall, it became modified to form the musculi adductor hyomandibularis and levator and adductor operculi. These three muscles of the Holostei and Teleostei are, accordingly, together, the serial homologue of the levatores arcuum branchalium in their own branchial arches, and the homologue of the dorsal portion of the hyal constrictor superficialis of the Selachii. The branch of the nervus facialis that innervated these hyal muscles, lying primarily on the anterior (external) surface of the constrictor of the arch, would naturally have followed the muscles, and so come to lie internal to the dorsal end of the hyomandibula. The

muscles would naturally retain their primitive relations to the vena jugularis, and when they acquired, by their dorsal ends, insertion on the neurocranium, that insertion would be dorsal to the vein; and such I find to be the relations of the muscles to the vein in Amia, Lepidosteus, Polypterus, Polyodon, and several Teleostei that I have examined for this special purpose, with the single exception of Ameiurus. In Ameiurus the vein passes over the posterior edge of the adductor hyomandibularis, and then lies dorsal (external) to that muscle, Ameiurus thus being exceptional in this as also in several other cranial features (Allis, 1915, p. 566).

Vetter (1878, pp. 532–534), also, considered that these muscles of the Teleostei were derived from what corresponds to the dorsal portion of the constrictor superficialis of the hyal arch of the Selachii, but he said it was difficult to conceive the intermediate stages in such an extraordinary change of position. The development of the hyomandibula in the manner that I have suggested wholly removes this difficulty. The levatores arcuum branchialium were considered by Vetter to represent remnants of the musculi interbranchiales of the Selachii, this conclusion being evidently based on the assumption that the constrictores superficiales of the Selachii had entirely disappeared in the Teleostei, as he had previously concluded that they had disappeared in Chimæra and Acipenser.

In an earlier work I said (Allis, 1897, p. 751) that: "The adductor hyomandibularis is probably developed from a muscle comparable to one or more of the interarcual muscles of the branchial arches of selachians, and is thus homodynamous with the levators of the branchial arches of teleostomes, and not with the adductor mandibulæ. The adductor operculi and levator operculi, at least the latter, are derived from the interbranchial muscles of their arch, and are thus homodynamous with the levator arcus palatini, and not with the levator muscles of the branchial arches." These conclusions were based on my interpretation of Vetter's descriptions of the Selachii, and on the acceptance of his conclusion that the

constrictores superficiales had entirely disappeared in the Teleostei, but as, as I have fully explained in preceding pages, Vetter's descriptions of these muscles are not wholly correct, my deductions from them were also not wholly correct. In a recent work (Allis, 1915), still influenced by Vetter's descriptions, I suggested that the adductor hyomandibularis of the Teleostei might be the homologue of the inferior postspiracular ligament of the Selachii; but as the adductor hyomandibularis of the Teleostomi would then be the serial homologue of the adductores arcuum branchialium of the Selachii, this cannot be if my present conclusions are correct.

Edgeworth (l.c., p. 210) says that the retractor hyomandibularis of Acipenser, and the adductor hyomandibularis of Lepidosteus, Amia, and Salmo, are all derived from the anterior portion of the constrictor superficialis of the hyal arch of the Selachii, and that the musculus opercularis of Acipenser and Lepidosteus, and the adductor and levator operculi of Amia and Salmo, are derived from the posterior portion of that constrictor of the Selachii; which is in accord with my present conclusions. The levatores arcuum branchialium of the Teleostei are said by Edgeworth to be developed from the upper ends of the branchial myotomes, which is evidently correct, but he then further says that, because of this origin, these muscles of the Teleostei have no counterparts in the Selachii, unless it be in the musculus trapezius as described by him, which I consider incorrect.

The proximal (anterior) fibres of the ventral portion of the constrictor superficialis of the hyal arch must, primarily, have all been inserted on the ceratohyal, and, in the Selachii, they became connected with their fellows of the opposite side by a median ventral aponeurosis, and so formed a musculus interhyoideus which extended from one hyal arch to the other across the ventral surface of the head. But a more or less important portion of the fibres later here acquired, as in the dorsal portion of the constrictor, a secondary insertion on the mandibular cartilage of either side, and so became an

intermandibularis. Whether or not this intermandibularis, innervated by the nervus facialis, was overlapped externally by an intermandibularis derived from the corresponding portion of the mandibular myotome, and innervated by the nervus trigeminus, cannot be told from dissections of the adult, but it is certain that, in the adults of living fishes, these two muscles are indistinguishably continuous one with the other. There is, accordingly, question as to where one muscle ends and the other begins, and it is frequently asserted that that part of the muscle that is of mandibular origin has lost its primary innervation by the nervus trigeminus and secondarily acquired innervation by the nervus facialis. It is accordingly important to know the relations of the nervus facialis to these muscles.

The ramus hyoideus facialis, as shown in nearly all of Vetter's (1874), Ruge's (1897), and Luther's (1909) figures of the Selachii, leaves the external surface of the hyal constrictor to acquire a position between the musculi interhyoideus and intermandibularis and does not reappear on the external surface of the latter muscle. This is not, however, invariably the case, for in one of Luther's figures of Heptanchus (l. c. p. 75) so-called motor branches of the nerve are shown reappearing on the external surface of the intermandibularis near its anterior end, and in the same author's figures of Chlamydoselachus, Heterodontus, Squalus, and Etmopterus, small branches of the nerve are also shown reappearing on the external surface of the muscle, but it is not said that they are motor nerves, as in the case of Heptanchus. In Chlamydoselachus one of these small branches is shown re-entering the muscle. Ruge found no branch of the nervus trigeminus going to any part of the musculus intermandibularis in any of the fishes examined by him. Luther, on the contrary, found branches of that nerve going to, and apparently innervating, the anterior part of the intermandibularis in all of the Plagiostomi examined by him excepting only Chlamydoselachus and the Notidanidæ. In his earlier work (1909) he concluded, in accord with Fürbringer (1903) and

Ruge (1897), that when the intermandibularis is innervated wholly by the nervus facialis, a muscle of facialis origin has simply crowded out and replaced one of trigeminus origin, but in a later work (1913, p. 46) he concluded that the trigeminus muscle here persisted, but had secondarily acquired innervation by the nervus facialis. Because of the wide distribution of the innervation of certain fibres of the intermandibularis by the nervus trigeminus, he considers this to be an archaic feature in fishes.

In Chlamydoselachus, I find the musculi interhyoideus and intermandibularis forming a single continuous muscle-sheet which extends transversely from one side of the head to the other, without the intervention of a median aponeurosis. The posterior quarter, approximately, of this muscle-sheet is inserted, on either side, on the corresponding ceratohyal, while the anterior half is inserted wholly on the mandibula. Between these two parts of the muscle-sheet, and lying immediately anterior to a tendinous band which extends from the musculus adductor mandibulæ to the musculus interhyoideus (see Luther, 1909, fig. 1), I find, in all my specimens, the fibres of the remaining quarter of the sheet separated, for a short distance along each lateral edge, into deeper and superficial layers, the deeper (dorsal) fibres being inserted on the ceratohyal and the superficial (ventral) ones on the mandibula. The deeper layer lies external to the proximal (anterior) portion of the ventral end of the constrictor of the first branchial arch, but in large part separated from it by the hyal branchial rays and the hyobranchial gill pouch. The constrictor of the first branchial arch similarly overlaps and lies external to the constrictor of the second branchial arch. This overlapping of these muscles is well shown in Vetter's figure of Heptanchus (1874, Pl. 15, fig. 7), where the proximal fibres of the constrictores superficiales of the first and second branchial arches, are shown lying directly internal to the musculus interhyoideus.

There are accordingly here, in Chlamydoselachus and

Heptanchus, four muscle-sheets superimposed one above the other, the two internal muscles being wholly independent of each other and of the external ones, because of the intervening branchial pouches, but the two external muscles being fused to a greater or less extent with each other in the mid-ventral line. It might then be assumed that these two external muscles belonged the one to the hyal and the other to the mandibular arch, and that they had, because of the abortion of the intervening branchial cleft, partially fused with each other, as the overlapping constrictores of the hyal and branchial arches of Mustelus and certain other Selachii have, and as has already been described. The conditions in Chlamydoselachus and Heptanchus can, however, equally well represent two different stages in the change of insertion of a hyal muscle from the branchial bar (ceratohyal) of its own arch to that (mandibula) of the mandibular arch, similar to the change of insertion that takes place in the dorsal portion of the muscle and has just been described. The first assumption requires the further assumption that the overlapping muscle of mandibular origin has wholly, or in large part, lost its primary innervation by the nervus trigeminus and secondarily acquired innervation by the nervus facialis; and Chlamydoselachus, generally considered to be the most primitive of living Selachii, would present a more advanced stage, not only in the fusion of these two muscles but also in the secondary change of innervation, than any other selachian that I know of. The second of the two assumptions entails no secondary assumptions for its justification, excepting the readily acceptable one that part of a hyal muscle has secondarily acquired insertion on a mandibular cartilage, and Chlamydoselachus, if a primitive fish, would naturally show an early stage in the process. The innervation of the muscles in Chlamydoselachus favours the second assumption.

In this fish, Chlamydoselachus, in each of five specimens that I have examined, the nervus hyoideus facialis at first runs forward along the external surface of the posterior portion of the interhyoideus, and there gives off two or more

branches. These branches also at first lie on the extern surface of the posterior portion of the interhyoideus, and send branches to that muscle and to the adjacent portions of the continuous, dorso-ventral fibres of the constrictor superficialis; these branches anastomosing more or less with each other. When the nerve and its branches reach the region where the primarily single muscle-sheet separates, along its lateral edges, into a superficial intermandibularis and a deeper interhyoideus portion, they, in four of the five specimens examined, all perforate the muscle-sheet, either at that line of separation or immediately anterior to it, and acquire a position between the two sheets. In this position the several branches either remain independent or unite to form one or two nerves, and, in one specimen which was examined simply for the muscles and not the nerves, they are shown, in my drawings, always lying between the two muscles, internal to the one and external to the other. In the other three of these four specimens, which were more carefully examined, the nerve or nerves ran forward for a certain variable distance between the two muscles, sending branches to them, and then perforated the intermandibularis, this time from within outward, and, reaching its external surface, there ran forward nearly to its anterior end. At this point, all the branches again penetrated the muscle-sheet, which was here represented by the intermandibularis alone, and did not again reappear on its external surface. In several instances the mesial branches of the nerves of opposite sides fused in the median line, anterior to the interhyoideus portion of the muscle, to form a single median nerve which then entered the musculus intermandibularis and was not farther traced.

On one side of the fifth one of the five specimens a large branch of the nerve remained on the external surface of the muscle-sheet, the main nerve perforating the sheet and running forward in the manner above described. The large branch crossed onto the external surface of the musculus adductor mandibulæ, sent a large branch to anastomose with the nervus mandibularis trigemini, and then itself turned

antero-mesially to reach and penetrate the anterior portion of the musculus intermandibularis. On the other side of the head of this same specimen, what was apparently the corresponding branch was given off while the main nerve was on the internal surface of the intermandibularis, and, having perforated that muscle from within outward, it joined and anastomosed with the latero-sensory nerve that innervates the sense organs of the hyomandibular line. No branch was noticed later leaving the latero-sensory nerve to go to the musculus intermandibularis, but as the dissection was made without any thought of there being such a branch it is probable that it existed but was overlooked. No branch of the nervus trigeminus was found going to any part of the muscle-sheet in any of my specimens. Luther (1909) shows a branch of this latter nerve going to the anterior end of the muscle, but he considered it to probably be a sensory and not a motor nerve.

The nervus hyoideus facialis must primarily have lain, in all the Selachii, along the anterior (external) surface of all the muscles it innervates that are derived from the myotome of its own arch, that being the position in which all the branchial nerves are found, and it does actually lie external to the interhyoideus in all of the five specimens of Chlamydoselachus above described. It, however, lies, in four of those five specimens, external to certain portions of the intermandibularis, but internal to certain other portions. If this intermandibularis muscle be developed from the myotome of the hyal arch, this difference in the relations of the nerve to the muscle can be naturally explained, as in the dorsal portion of the constrictor of this arch, by the assumption that certain of the fibres of the muscle, which were primarily inserted on the ceratohyal, had secondarily acquired insertion on the mandibula by passing external to the nerve as that nerve ran forward near the ventral (morphologically posterior) edge of the mandibula, while in other cases the muscle retained its primitive position internal (posterior) to the nerve. This explanation would, however, not apply if the intermandibu-

laris were of mandibular origin, for the muscle would then have lain primarily anterior and hence external to the nervus facialis, and it is difficult to conceive how certain portions of it, still retaining their primary insertion on the mandibula, could have shifted from this primarily anterior and external relation to the nerve to a posterior and hence internal relation to it. And as the muscle in no way lies in the path of, or interferes with the nervus facialis, it is difficult to conceive a reason for the perforation of the muscle by the nerve.

The interhyoideus and intermandibularis muscles of Chlamydoselachus could accordingly both be of facialis origin, so far as the relations of nerve and muscle are concerned, but in all probability only that portion of the intermandibularis that lies anterior to the point where the nervus facialis definitely disappears from its external surface could be of mandibular origin. And if this portion of the muscle be of mandibular origin, as several authors have maintained, I consider it certain that it is innervated by a branch of the nervus mandibularis trigemini, and that that branch has simply been missed in dissections, my own included. That it is possible that this nerve has been so missed is shown by the fact that in Heptanchus, where Fürbringer and Luther both found the intermandibularis innervated by the nervus facialis alone, my assistant, Mr. John Henry, finds, on both sides of the head of one of three specimens of this fish that were examined, a branch of the nervus mandibularis trigemini going to the intermandibularis in a position strictly comparable to that shown by Luther in several of the Selachii examined by him, while in the other two specimens it was not found.

Edgeworth says that the musculi interhyoideus and intermandibularis, apparently wherever found in the vertebrate series, are not developed from the myotomes of their respective arches, but from related portions of the wall of the cœlomic cavity, and that they accordingly have no homologues in the branchial arches. According to him (loc. cit., p. 178): "The cephalic cœlom disappears in the mandibular and hyoid

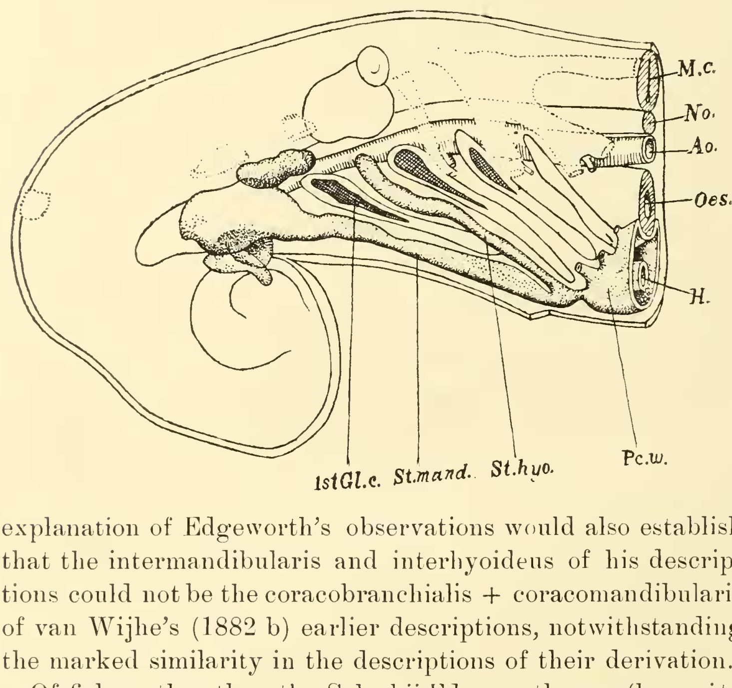
segments early in development, and its walls develop into the intermandibularis and interhyoideus, which are at first continuous with the mandibular and hyoid myotomes. The lower ends of the branchial myotomes separate from the wall of the branchial portion of the cephalic cœlom, and they develop into the branchial muscles. No muscles are directly formed from the wall of the branchial portion of the cephalic cœlom, which subsequently retreats from the head." This strikingly recalls van Wijhe's description of the development of the coracobranchialis + coracomandibularis muscles in these same fishes, but it seems certain that the observations of these two authors do not relate to the same muscles. Of the intermandibularis of Scyllium Edgeworth says (loc. cit., p. 180): "The intermandibularis (Cs_2 of Vetter, C_2mv of Ruge) is formed from the ventral portion of the mandibular cavity, which, as mentioned above, does not meet its fellow in the mid-ventral line, but passes backwards ventro-median to the ventral end of the hyoid cavity to open into the fore end of the cephalic cœlom." Here, in Scyllium, the intermandibularis is thus definitely said to arise from the mandibular cavity and hence not from a part of the cephalic cœlom, which would seem to be in direct contradiction to the statement just previously made. Edgeworth then further says: "It results from this that there is no developmental stage in which the intermandibularis lies altogether in front of the interhyoideus. It gradually extends backwards, underlying the interhyoideus, so that in 23 mm. embryos its hinder end lies posterior to the ventral end of the ceratohyal."

Luther (1909, p. 97) has already made brief reference to this development of the intermandibularis and interhyoideus from parts of the cephalic cœlom, as set forth in an earlier work of Edgeworth's (1902) which I have not been able to consult, and he, Luther, expresses much doubt as to its being correct, an opinion which I strongly share. My reasons for considering it incorrect can be best explained by reference to Scammon's (1911) figures of the head somites in embryos of

Squalus acanthias. In fig. 20 of that work Scammon gives a reconstruction of the head somites in a 9 mm. embryo of Squalus, and I have reproduced it in the accompanying Text-fig. 1. In this figure it is seen that while the cœlomic cavity might properly be considered to be prolonged into the short united portion of the hyal and mandibular stalks, and even beyond the hyal stalk for a short distance into the ventral end of the mandibular stalk, it can no more be considered to be prolonged into the basal portion of the hyal stalk than also into the basal portions of the stalks of the branchial myotomes. The case is strictly similar to that of the truncus arteriosus and the afferent arteries that arise from it. The truncus arteriosus cannot be considered as in any way continued into any of these arteries excepting only into the afferent mandibular artery. With regard to this latter artery there is no line of demarcation to indicate where the truncus arteriosus ends and the mandibular artery begins, and in my discussion of these arteries in embryos (Allis, 1908) I assumed that the basal portion of the afferent mandibular artery represented an anterior prolongation of the truncus arteriosus. The cavity designated as the hyal cephalic cœlom in Edgeworth's Text-fig. 1, showing a transverse section of a 7 mm. embryo of Scyllium, is then certainly a part of the hyal stalk, and the fact that the interhyoideus muscle, developed from this part of the stalk, is said to be at first continuous with the hyal myotome would seem to be of greater significance than the further fact, to which Edgeworth gives the greater significance, that this part of the stalk does not separate from the wall of the cœlomic cavity before developing into muscle fibres, as the stalks of the myotomes in the branchial region are said to do. The so-called mandibular cephalic cœlom of this same Text-figure of Edgeworth's might, however, be considered to be a part of the cephalic cœlom, for, as in the case of the afferent mandibular artery, there is no line of demarcation to indicate where the cephalic cœlom ends and the mandibular stalk begins. But if the musculus interhyoideus is developed from the ventral portion of the hyal

myotome and not from a part of the cephalic cœlom, as above explained, then the musculus intermandibularis must be developed from a corresponding portion of the mandibular myotome, for Edgeworth says (loc. cit., p. 226) that these two muscles are serially homologous. This conclusion is inevitable if the premises are correct, and the intermandibularis, although lying actually, in sections, ventral to the interhyoideus, would lie morphologically entirely in front of that muscle. This

Text-fig. 1.



explanation of Edgeworth's observations would also establish that the intermandibularis and interhyoideus of his descriptions could not be the coracobranchialis + coracomandibularis of van Wijhe's (1882 b) earlier descriptions, notwithstanding the marked similarity in the descriptions of their derivation.

Of fishes other than the Selachii Edgeworth says (loc. cit., p. 209) that, in 8 mm. embryos of Acipenser, the hyal muscles " consist of a hyoid myotome, the anterior part of which is inserted into the upper end of the hyoid bar, forming a levator hyoidei, and the posterior part of which forms a dorso-ventral sheet—homologous with C_2vd of selachians—

continuous with the posterior part of the interhyoideus, whilst the anterior part of the interhyoideus is inserted laterally into the hyoid bar." And also (loc. cit., p. 210) that: "The fore part of the interhyoideus of Acipenser forms the hyohyoideus inferior (Cs_5 of Vetter), the hinder part, i. e. the lower part of C_2vd, forms a constrictor operculi (Cs_3 and Cs_4 of Vetter). In Polypterus the condition is similar. In Lepidosteus, Amia and Salmo, the fore part forms the hyohyoideus inferior; the hinder part becomes attached laterally to the hyoid bar (only partially so in Lepidosteus) and forms the hyohyoideus superior."

In Amia, the superior or deeper, and the inferior or superficial portions of the geniohyoideus of my descriptions of that fish are respectively called by Edgeworth (loc. cit., p. 210) the musculus hyomaxillaris and the musculus intermandibularis posterior. The musculus hyomaxillaris, as above defined by Edgeworth, is said by him to be differentiated from the "upper edge" of the hyohyoideus inferior, but comparison with the adult shows that this so-called upper edge of that muscle must be the dorsal edge as seen in transverse sections of embryos, and hence morphologically the anterior edge of the muscle. In Lepidosteus and Acipenser these same fibres of the hyohyoideus inferior are said to form a hyomaxillaris ligament, and this ligament is said (loc. cit., p. 212) to be the ligamentum mandibulo-hyoideum of van Wijhe's (1882a) descriptions of the adults of these fishes. But there is evidently some error or oversight here, for a ligamentum mandibulo-hyoideum is described by van Wijhe in Amia, as well as in Lepidosteus and Acipenser, and hence coexists in the former fish along with the musculus hyomaxillaris of Edgeworth's descriptions. A further difficulty is that the musculus hyomaxillaris of Amia is said (loc. cit., p. 223) to be a serial homologue of the interarcuales ventrales of the branchial arches of that fish, notwithstanding that the former muscle is said to be derived from the cephalic cœlom, as already explained, and the latter muscles to be developed from the ventral ends of the branchial myotomes. Edgeworth calls

attention to this, and explains it by saying that the corresponding muscle in Alytes, Rana, Pelobates, and Lepus is formed from the ventral end of the hyal myotome, and that this method of formation is probably the primitive one.

The intermandibularis of all teleostoman embryos is said by Edgeworth (loc. cit., p. 187) to form at first, with its fellow of the opposite side, a transverse muscle attached laterally to Meckel's cartilage, and it is later said (loc. cit., p. 202) that a comparison of the various forms of the muscle shows that this condition of a transverse sheet is the primitive one for the muscle. It is, however, immediately afterwards said that this condition of a transverse sheet persists (" exists ") only in Salmo. Edgeworth further says (loc. cit., p. 280) : " (3) The intermandibularis anterior and posterior (the latter called ' inferior geniohyoid ' by Allis) of Amia are innervated by both the fifth and seventh (Allis). (4) The hyo-maxillaris of Teleostomi, developed in the hyoid segment, is in some, e. g. Menidia (Herrick), wholly innervated by the seventh ; whereas in others, e.g. Esox (Vetter), Salmo, its hinder part is innervated by the seventh and its fore part by the fifth ; and in Amia (Allis) it is innervated by the fifth and seventh."

These latter two statements would seem to imply that certain of the individual fibres of the muscles referred to in Amia were innervated at the same time by two different nerves, and that they were in process of losing their normal innervation by the nerve of their segment of origin and secondarily acquiring an innervation by a nerve of another segment. If this be the meaning of the statements, the reference to Amia is unfortunate, and is apparently based on the literal acceptance of the heading of one of the sections of my work on that fish without any consideration of the accompanying text. That heading is (Allis, 1897, p. 559) : " Muscles innervated by both the Trigeminus and Facialis," which, literally accepted, might have the meaning that Edgeworth apparently gives to it. But in the text (loc. cit., p. 613) it is carefully explained that the muscles in question are innervated by branches of a nerve formed by the anastomosis of trigeminus and facialis branches

which run directly into each other and so form a complete circuit in which it is impossible to tell where the one nerve ends and the other begins. In the General Summary it is further said (loc. cit., pp. 744–5) that the ramus maxillaris inferior trigemini probably innervates the musculus intermandibularis and all, or a part, of the inferior division of the geniohyoideus, and that the ramus hyoideus facialis probably innervates the superior division of the geniohyoideus, and a part, at least, of the inferior division of that muscle. The innervation, in each case, is only given as probable, and there is no slightest suggestion of any part of either of the muscles being innervated, at the same time, by both the nerves.

Mandibular Arch.

Dohrn says (1885, p. 13) that, in selachian embryos, a muscle is developed from a myotome that comes from the mandibular arch (eines Muskelschlauches welcher vom Kieferbogen kommt), and that this muscle corresponds to the ventral portion of the constrictor superficialis of the hyal arch. There is, as already explained, some question as to whether Dorhn considered a part of this muscle to be the homologue of the coracobranchialis of the branchial arches, but it is certain that the myotome, said to come from the mandibular arch, must be the ventral end of the mandibular myotome, and that the muscle said to be developed from it must be that part of the musculus intermandibularis of the adult that is primarily, if not actually, innervated by the nervus trigeminus. Edgeworth (1911) says, as has already been fully explained and discussed, that the myotome of the mandibular arch only extends to the ventral edge of the musculus adductor mandibulæ, and that the musculus intermandibularis is developed from the walls of the cephalic cœlom. There is thus here marked difference of opinion.

Accepting Dohrn's observations as correct, and assuming that there was primarily a premandibular arch separated from the mandibular arch by a visceral cleft, there must

have been primarily, in the mandibular arch as in the hyal and branchial arches, a single continuous constrictor muscle that had a dorso-ventral extent equal to that of the constrictor of the hyal arch. Branchial rays also probably primarily existed in this arch as in the more posterior arches, for remnants of them are said to be still found in certain recent fishes. Branchial lamellæ were then quite probably also developed in this arch as in the more posterior ones, and were probably found on the anterior as well as the posterior surface of the arch.

The conditions in this mandibular arch would then have been similar to those in the hyal and branchial arches, and, such being the case, there seems no good reason why, when the visceral arches all began to assume a position oblique to the axis of the body, a small adductor muscle should not have been cut out of the proximal edge of the constrictor of this arch, as it is said to have been cut out of the constrictores of the branchial arches, and as I assume that it was also cut out of the constrictor of the hyal arch.

When the hyomandibular cleft later became reduced to the small existing spiracular canal, the mandibular branchial diaphragm, which must primarily have existed as in the hyal and branchial arches, would necessarily have gradually ceased to be formed excepting as it may still be represented in some part of the anterior wall of the spiracular canal. Because of this gradual reduction and final almost complete disappearance of the branchial diaphragm of this arch, the middle portion of the long constrictor superficialis of the arch was necessarily forced over onto the anterior (lateral) surface of the cartilaginous bar of the arch, and it carried with it the nerve of the arch, and probably also the anterior efferent artery of the arch (Allis, 1916), this nerve and artery primarily lying anterior to the constrictor muscle, as they actually do in the branchial arches of living Selachii. The afferent mandibular artery and the branchial rays, both lying posterior to the constrictor muscle, were not so carried forward, and retained their primitive positions on

or near the morphologically external but actually posterior edge of the cartilaginous bar of the arch. The posterior efferent artery, also, was not affected by this change in position of the constrictor muscle, but it later underwent reduction or abortion in its ventral portion, while dorsally it persisted and retained its normal position posterior to the spiracular cartilage, that cartilage representing either the dorsal extrabranchial of the arch or one or more of the branchial rays. That any of the branchial rays of this arch could, in such a shifting of the constrictor, have acquired the positions of the labial cartilages seems quite impossible.

The long musculus constrictor superficialis, having acquired this position on the anterior (lateral) surface of the cartilaginous bar of its arch, was later more or less completely cut in two at the places where it crossed the palatoquadrate and the mandibula. The portion so cut out of the middle of the constrictor was then added to the small, pre-existing musculus adductor to form the large and powerful adductor of the adults of living fishes, while the ventral portion formed the intermandibularis and the dorsal portion the levator of the arch. Certain of the fibres of the original constrictor were, however, quite certainly not thus cut through at the places where they crossed the palatoquadrate and mandibula, for certain of them still extend, in the adults of living fishes, the full length of the arch. This is markedly the case in certain of the fibres of the musculus spiracularis of Astrape. This muscle is said by Luther (1909, p. 14) to be developed from the posterior fibres of the dorsal portion of the primitive constrictor of the arch and to have a ventral prolongation which lies along the internal surface of the mandibula (kieferapparat) and extends as far as the symphysis of the mandibulæ, there uniting with its fellow of the opposite side. This ventral prolongation is a feeble muscle, of no apparent functional importance, and certainly cannot be a secondary formation, as Luther considers it to be. It must, on the contrary, represent a persisting remnant of a distal part of the primitive constrictor which, when the

branchial rays aborted, slipped onto the posterior, instead of onto the anterior, surface of the cartilaginous bar of the arch, and so, not crossing that bar, was not cut in two as the other fibres of the constrictor were.

In certain other Batoidei, the musculus spiracularis is said by Luther to have a less extensive ventral prolongation than in Astrape, being said to extend either to the ventral end of the hyomandibula, to the abdental edge of the mandibula, to the ceratohyal, or to the dorsal fascia of the musculus coraco-mandibularis. In Astrape and Torpedo, certain fibres of the muscle are said to be inserted on, and others to arise from, the spiracular cartilage, that cartilage thus lying between dorsal and ventral portions of the muscle; and as I have lately shown (Allis, 1915) that this cartilage of these fishes is quite certainly the dorsal extrabranchial of the mandibular arch, the muscle thus has the relations to this cartilage that the branchial constrictores superficiales of certain Selachii have to the dorsal extrabranchials of their respective arches.

Other portions of the primitive constrictor apparently lost only their ventral, intermandibularis, portion, retaining their full lengths dorsal to that muscle. Such portions are apparently found in the second and third divisions of the levator maxillæ superioris of my descriptions of Amia, and in the levator labii superioris of certain of the Batoidei, all of which muscles extend, with their tendinous ends, from the neurocranium to the abdental edge of the mandibula. The levator labii superioris of the Batoidei, called by Luther the musculus præorbitalis, is said by that author to usually extend only to the angle of the gape of the mouth and to there be inserted in the aponeurotic septum of the adductor mandibulæ, but it may have a ventral ligamentous prolongation, or even a large muscle belly, which extends beyond the angle of the gape and is inserted, with the mandibular portion of the adductor, on the mandibula. In certain of the Batoidei it is even said that the tendinous ventral end of the muscle is practically continuous with the lateral edge, and hence

morphologically dorsal end, of the musculus intermandibularis, the constrictor fibres in these fishes thus apparently having retained their full primitive lengths.

Luther (1909, p. 49) considers the levator labii superioris (præorbitalis) to have been primarily simply a bundle of the adductor mandibulæ that had its origin at a high level on the neurocranium, anterior to the eyeball. The more ventral origin of this muscle, from the antorbital process, found in Chlamydoselachus and certain other Plagiostomi, he considers to be secondary and correlated either to an enlarged eyeball or to a large gape of the mouth with the angle of the gape far posterior, the muscle here secondarily becoming a "Spreizer" of the articulating ends of the upper and lower jaws. The eyeball is considered by him (loc. cit., p. 36) to have been the chief one of these two causes of the splitting off of this bundle from the remainder of the adductor mandibulæ, and if this be so, the eyeball thus being assumed to have lain in the path of the muscle-fibres of the arch as they pushed dorsally to acquire insertion on the neurocranium, it would seem as if this split in the muscle must have begun at the dorsal end of the primitive constrictor and not at the dorsal end of that middle portion of that muscle that is usually considered to, alone, have given origin to the adductor mandibulæ. The dorsal portion of the præorbitalis would then contain the anterior fibres of the dorsal muscle, Csd_2, of Vetter's descriptions, and where the præorbitalis extends beyond the angle of the gape the split that separates it from the adductor would extend from the dorsal end of the constrictor as far at least as the ventral end of the adductor. Such an extensive split in this myotome can certainly not be explained simply by the eyeball having caused the dorsal fibres of the constrictor to diverge anteriorly and posteriorly in order to acquire a dorsal attachment on the neurocranium, and if Luther is correct in his conclusion that this muscle had primarily its origin at a high level on the neurocranium, a much more rational explanation would seem to be that this muscle belongs to a premandibular arch. The recorded innervation of the muscle,

and the embryological evidence are, however, both against this supposition.

Edgeworth (1911) derives both the levator labii superioris of the Plagiostomi and the four divisions of the levator maxillæ superioris of my descriptions of Amia, directly from the adductor mandibulæ, and from that portion only of the primitive mandibular constrictor. Luther also derives these four muscles of Amia directly from the adductor mandibulæ; and he proposes for the first and second divisions of the muscle the name musculus adductor mandibulæ parabasalis, because of their partial origin from the lateral wing of the parasphenoid (parabasalis, Gaupp), and for the third and fourth divisions of the muscle the names musculus adductor mandibulæ præorbitalis and musculus nasalis. Edgeworth considers the muscles of Amia to all be upgrowths of the internal and deeper portion, only, of the adductor of the adult, and suggests that they be named in terms of that internal adductor. The myotome of this arch is, according to him, definitely and entirely cut into dorsal and ventral portions where it crosses the dorsal edge of the palatoquadrate, these two parts remaining always distinct and separate, while the intermandibularis is, as already stated, developed wholly from the walls of the cephalic cœlom. Until the derivation of these muscles is definitely known it would seem best not to give them names based wholly or largely upon it.

There remains now only the aponeurotic septum of the adductor mandibulæ to be considered. Fürbringer (1903, p. 383), considered this aponeurosis to be of secondary origin and of no great morphological significance, it being developed, in fishes where the mouth opening had a pronounced posterior extension, simply in order to give space for suitable development of the belly of the adductor. Luther (1909, p. 61) thinks this an insufficient reason for the development of the aponeurosis, and considers it to have been secondarily developed, after the development of the levator labii superioris (præorbitalis), in order to furnish an attachment for that muscle on the quadrato-mandibular joint, and so facilitate its

action as a protractor of the palatoquadrate and also as a spreader (Spreizer) of the articular ends of the jaws. I consider the aponeurosis to have been developed wholly independently of either of these two functions. In my opinion, a small adductor muscle had already been differentiated in this arch before the remainder of the constrictor began to slip over onto the anterior surface of the cartilaginous bar of the arch. There was, at this period, quite certainly not sufficient space between the relatively close fitting integument of the arch and the cartilaginous bar to permit this large and long constrictor muscle to immediately assume the position that the adductor actually has in the adults of living fishes, and the small adductor already occupied the angle between the two elements of the cartilaginous bar. Certain of the fibres of the constrictor accordingly quite certainly acquired attachment on the internal surface of the dermis at the angle of the gape These fibres would immediately act as an adductor when the mouth was widely open, but when the mouth was closed, or even nearly closed, they would act primarily as a protractor anguli oris, and secondarily as an abductor of the arch ; for, being attached to the dermis at the angle of the gape, and the dermis being fixed, any contraction of the muscle would necessarily tend to open the mouth. This would evidently be of advantage to the fish, for, in the early stages of the development of the mouth, there was probably no other abductor mechanism, the ventral longitudinal muscles not yet having been developed. The fibres so inserted, increasing in number and importance, would, as the adductor muscle developed and a cheek was formed, pinch off the subdermal tissues to which they were attached and an aponeurosis such as is actually found in Chlamydoselachus, and will be fully described in my later work, would almost inevitably arise. If these fibres did not become attached to the dermis they would, in certain cases, become tendinous as they passed across the angle of the gape, as they do when passing over the extrabranchials and the middle rays of the branchial

series in the branchial arches of certain fishes (Vetter, 1874), and the condition found in the adults of many fishes would arise. If such fibres should then separate from the remaining fibres of the adductor, a musculus præorbitalis with dorsal and ventral muscle bellies, such as is described by Luther in certain of the Plagiostomi, would arise. And if the ventral, mandibular portion of the muscle became wholly tendinous, the condition found in the first and third divisions of the levator maxillæ superioris of my descriptions of Amia might arise. The aponeurosis would naturally tend to be developed only where the mouth had a marked posterior extension and the opening of the gape was long. According to Luther (loc. cit., p. 62) the aponeurosis and the muscle Addγ of Vetter's descriptions vary inversely, a marked development of the one being associated with a feeble development of the other, and he attributes this to the fact that a strongly developed Addγ would act as a spreader of the jaws, and the musculus præorbitalis, being relieved of that function, there would be no call for an aponeurosis. As I attribute the development of the aponeurosis to a totally different cause it does not seem to me that this applies.

General Summary.

The primitive condition of the muscles related to the visceral arches of the gnathostome fishes was, as Vetter long ago concluded, a simple constrictor muscle in each arch, and associated with this muscle there was a branchial bar which lay internal to the muscle.

From this simple primitive condition two distinctly different lines of descent are indicated by later differentiations of the muscles, and these differing differentiations are associated with, and caused by, two distinctly different forms of branchial bar in the branchial arches. One of these two lines of descent is represented by the Teleostomi and the other by the Plagiostomi, the Holocephali and Dipneusti apparently occupying somewhat intermediate positions.

In the Teleostomi, the four typical elements of each branchial bar of recent fishes lie, approximately, in a single plane, and this must have been their primitive relation to each other. Primarily this plane must have been transverse to the axis of the body, but it later became inclined to that axis. Associated with this form of arch the branchial filaments of the gill-bearing arches are supported by cartilaginous or osseous rods. In the hyal arch there are, in addition, osseous branchiostegal rays which lie anterior to the modified constrictor of the arch.

In the Plagiostomi, the dorsal and ventral elements of each branchial bar are directed postero-mesially at a marked angle to the middle elements of the bar, these latter elements lying, as in the Teleostomi, in a plane inclined to the axis of the body. A sigma form of bar is thus produced, and associated with it there are cartilaginous branchial rays in all the gill-bearing arches. These cartilaginous rays all lie, primarily, posterior to the constrictor muscle of the related arch, but the muscle fibres may later become in part inserted on them.

In the Holocephali and Dipneusti, the dorsal elements of the branchial bars are directed postero-mesially, as they are in the Plagiostomi, while the ventral elements are directed antero-mesially, as in the Teleostomi. In the Holocephali there are, according to Vetter, cartilaginous rays both in the hyal and the branchial arches, and the visceral muscles as described by him seem plagiostoman in character. In the Dipneusti there are cartilages in the hyal arch that are considered by Fürbringer to be branchial rays, but there are neither branchial rays nor supporting rods to the branchial filaments in the branchial arches; and the branchial muscles are teleostoman in character.

The constrictor muscle is found in a more primitive condition in the Selachii than in any others of the gnathostome fishes. Because of the sigma form of branchial bar in these fishes, the proximal (anterior) edge of the constrictor of each branchial arch has slipped forward over the anterior edge of the middle, posteriorly-directed angle of the sigma, and

backward over the posterior edges of the dorsal and ventral, anteriorly-directed angles of the sigma; and from the parts of the constrictor that cross or span these three angles are differentiated, respectively, the adductores arcuum branchialium, the arcuales and interarcuales dorsales, and the coracobranchiales of Dohrn's descriptions of embryos. These latter muscles are simply the proximal (anterior) portions of the ventral ends of the primitive constrictores of the branchial arches, they are of branchial origin, are innervated by branches of the nervus vagus of the arch to which they belong, and they coexist, in the adult, with the coracobranchiales of Vetter's descriptions. The latter muscles are said, by both Dohrn and Edgeworth, to be derived from the ventral ends of the branchial myotomes, but their innervation, in the adult, by spinal or spino-occipital nerves, their relations to the other hypobranchial muscles, and the marked want of accord in the descriptions of their development, all warrant the conclusion that they must be of spinal origin.

The distal (posterior) portion of the constrictor muscle of each branchial arch of the Selachii, the so-called constrictor superficialis, lay primarily not only on the anterior surface of the branchial rays of its arch, but also on that surface of the extrabranchials of its arch; and, in the adults of recent fishes, its dorsal and ventral ends turn posteriorly, to a greater or less extent, across the dorsal and ventral edges, respectively, of the next posterior gill-pouch. When the constrictor contracted, the muscle was accordingly stretched across the extrabranchials of its arch, and certain of the muscle fibres, in certain fishes, were there cut in two by acquiring insertion on the extrabranchials. Other fibres simply became tendinous where they passed over the extrabranchials, and so there gave rise to more or less pronounced linear aponeuroses, or so-called septa. That part of each constrictor that lay between the dorsal and ventral extrabranchials of its arch thus became more or less cut out of the primarily continuous constrictor, and formed the musculus interbranchialis. This muscle is never found definitely

differentiated in the hyal arch, but indications of the beginnings of its differentiation may there be found.

In the hyal arch of the Selachii, an adductor muscle was probably developed exactly as in the branchial arches, but it was later transformed into the inferior postspiracular ligament. Arcualis and interarcualis muscles are not found in this arch of the adult, but Dohrn says that they are represented, in embryos, by ligaments, which he does not, however, describe. The coracobranchialis of Dohrn's descriptions of the branchial arches is not differentiated in this arch. The dorsal and ventral portions of the constrictor tend to separate into deeper and superficial layers, as Ruge has stated, the deeper layer retaining its primitive insertion on the cartilaginous bar of its arch, while the superficial layer acquires a secondary insertion on the cartilaginous bar of the mandibular arch.

In the Batoidei, an adductor muscle was not differentiated in the hyal arch, and there is accordingly, in these fishes, no inferior postspiracular ligament. The proximal (anterior) portion of the primitive constrictor of this arch is differentiated into the levator and depressor hyomandibularis, and probably also the depressor mandibulæ, these muscles replacing the adductor, arcualis, interarcualis, and Dohrn's coracobranchialis of the Selachii. The so-called septa in these fishes are probably similar to those in the Selachii, but this cannot be definitely determined from existing descriptions.

In the mandibular arch of the Selachii, a small adductor muscle was probably developed exactly as in the more posterior arches. Later, because of the suppression of the branchial diaphragm related to this arch, excepting as it may be represented in the anterior wall of the spiracular canal, the entire constrictor muscle was forced, in its middle portion, onto the anterior surface of the cartilaginous bar of its arch, and, acquiring insertion on the palatoquadrate and mandibula, where it crossed their lateral edges, was added to the small, pre-existing adductor, and so gave rise to the

large adductor mandibulæ actually found in the adult. From those portions of the primarily continuous constrictor that lay dorsal and ventral, respectively, to the palatoquadrate and mandibula, the musculi levator maxillæ superioris and intermandibularis were developed. The musculus levator anguli oris was probably derived from the anterior edge of the united levator and adductor muscles before they became separated from each other. The musculus intermandibularis underwent relative reduction, and, in the adults of recent fishes, is largely crowded out and replaced by those superficial fibres of the hyal constrictor that have secondarily acquired insertion on the mandibula. The relations of the nervus hyoideus facialis to the muscle fibres thus inserted on the mandibula is against the view that those fibres that are of mandibular origin have lost their primitive innervation by the nervus trigeminus and secondarily acquired innervation by the nervus facialis.

The posteriorly directed dorsal and ventral ends of the hyal and branchial constrictores of the Selachii always overlap, to a greater or less extent, the next posterior constrictor. Where the ends of the constrictores are strongly inclined posteriorly, they may overlap two or more posterior constrictores, the fibres of the muscles then crossing the extrabranchials of those arches and there tending to become tendinous exactly as they do where they cross the extrabranchials of their own arches; a series of tendinous aponeuroses thus being formed in each constrictor. The overlapping muscles then fuse more or less completely with each other, and, as the linear aponeuroses related to each extrabranchial are superimposed and transverse to the muscle fibres, the continuous muscle-sheet formed by the fusion of the several constrictores is cut up into what have heretofore been considered to be separate segments, one related to each branchial arch and developed entirely from the myotome of that arch. These segments are, however, each formed by muscle fibres derived from two or more consecutive constrictors, and hence from a similar number of consecutive myotomes.

The dorsal portion of the constrictor of the ultimate branchial arch undergoes excessive development and becomes the musculus trapezius.

In the Teleostomi, each branchial bar, although inclined to the axis of the body as in the Selachii, continues to lie, approximately, in a single plane, and the dorsal and ventral ends of the constrictores do not turn posteriorly as in the Selachii. The pull of the constrictor, when contracting, did not, accordingly, tend to make the muscle slip, in the middle of its length, over the anterior edge of the branchial bar of its arch, but in certain of the branchial arches of the Ganoidei the proximal edge of the muscle slipped over the posterior edge of the branchial bar, and there gave rise to an adductor that is the functional equivalent but not the homologue of the adductor of the Selachii. The remaining fibres of the middle portion of the constrictor either later aborted or, possibly, became modified to form the radially arranged muscles related to the supporting rods of the branchial filaments. The dorsal and ventral ends of the constrictores became the levatores and the transversi and obliqui dorsales and ventrales. The levator of the ultimate arch is a slender muscle, and may secondarily acquire insertion on the shoulder-girdle. It is the homologue of the large musculus trapezius of the Selachii.

In the hyal arch of the Teleostomi, the constrictor persists to a greater extent than in the branchial arches. Its dorsal portion becomes the adductor hyomandibularis and the adductor and levator operculi, these muscles, together, being the equivalent of the levatores of the branchial arches of the Teleostomi and of the dorsal ends of the constrictores of the Selachii.

The ventral portion of the constrictor of the ultimate, or fifth, branchial arch of the Teleostomi is modified to form the musculi coracobranchiales or pharyngoclaviculares, these muscles of these fishes thus being branchial muscles, and hence probably not the homologues of the coracobranchiales of the Selachii. They always retain, in all fishes that I have

been able to examine, their primitive innervation by branches of the nervus vagus. The dorsal portion of the constrictor of this arch forms, as already stated, the fifth levator muscle, which is the homologue of the musculus trapezius of the Selachii.

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EXPLANATION OF PLATES 21 AND 22.

Illustrating Mr. Edward Phelps Allis's paper on "The Homologies of the Muscles related to the Visceral Arches of the Gnathostome Fishes."

Reference Letters.

Add. Musculus adductor mandibulæ. *Add. br. I–IV.* Musculi adductores arc. branch. of I–IV branchial arches. *ahy.* Afferent artery of hyal arch. *ap. I–IV.* Linear aponeuroses related to the first to fourth gill clefts. *Arc. I–IV.* Musculi arcuales of I–IV branchial arches. *bcl. I–V.* First to fifth branchial clefts. *BH.* Basihyal. *bp. I–V.* First to fifth branchial pouches. *BR. hy.* Branchial rays of hyal arch. *Carc.* Musculus coracoarcualis communis. *CB. I–II.* Ceratobranchials of first two branchial arches. *Cbr. I–V.* Musculi coracobranchiales of I–V branchial arches. *CH.* Ceratohyal. *Chy.* Musculus coracohyoideus. *Cmd.* Musculus coracomandibularis. Cs_{2-6}. Musculi constrictores superficiales of second to sixth visceral arches. *ex. I–IV.* Extrabranchials of I–IV branchial arches. *ex. h.* Extrabranchial of hyal arch. *HMD.* Hyomandibula. *hmf.* Nervus hyoideo-mandibularis facialis. Ibr_{3-6}. Musculi interbranchiales of third to sixth visceral arches. *Ihy.* Musculus interhyoideus. *Imd.* Musculus intermandibularis. *lc.* Lateral canal of body. *Lhmd.* Musculus levator hyomandibularis. *m.* Dorsal muscles of trunk. *MD.* Mandibula. *mlt.* Nervus mandibularis trigemini. *pc.* Pericardial cavity. *S.* Shoulder-girdle. *sp.* Spiracle. *Tr.* Musculus trapezius. *vj.* Vena jugularis.

PLATE 21.

Fig. 1.—Lateral view of the head of a 42-cm. Scyllium canicula, with skin removed to show the branchial muscles. × 1½.

Fig. 2.—The same. The constrictores superficiales cut along their dorsal edges and turned forward and downward so as to expose the underlying structures. × 1½.

Fig. 3.—Ventral view of the same. The constrictor superficialis of the hyal arch cut through in the mid-ventral line and turned forward on the right-hand side of the figure. × 1½.

Fig. 4.—The same; a deeper dissection. On the left-hand side of the figure the hyal constrictor has been cut through near its lateral edge and turned forward. On the right-hand side it has been wholly removed, and the ceratohyal turned slightly forward. On both sides

of the figure the ventral portions of the constrictores of the first three branchial arches have been cut away up to the line of the extrabranchial of the arch, and on the right-hand side of the figure the ventro-posterior portions of the gill pouches have been cut away so as to expose the underlying constrictor of the next posterior arch. In the fourth branchial arch a piece has been cut out of the constrictor of the arch ($Cs._6$) so as to expose the fifth gill pouch. The musculi coracomandibularis, coracohyoideus, coracobranchialis I, and coracoarcualis have been cut through and removed. $\times\ 1\frac{1}{2}$.

PLATE 22.

Fig. 5.—The same; a still deeper dissection. The ceratohyal and the extrabranchial of the first branchial arch both removed on the right-hand side of the figure. $\times\ 1\frac{1}{2}$.

Fig. 6.—The same; a still deeper dissection. The extrabranchial of the second branchial arch also removed on the right-hand side of the figure. $\times\ 1\frac{1}{2}$.

Fig. 7.—Lateral view of the branchial region of the same. The constrictores superficiales of the hyal and first three branchial arches, and the four related gill-pouches removed, but the cut dorsal ends of the extrabranchials of the first three branchial arches left in place. $\times\ 2$.

Fig. 8.—Lateral view of the head of a 43-cm. Mustelus. The skin removed so as to expose the constrictores superficiales of the hyal and branchial arches. $\times\ 2$.

Fig. 9.—The same. The continuous sheet formed by the constrictores superficiales has been cut along its dorsal edge, and those fibres of each musculus interbranchialis that are inserted in the related linear aponeurosis have also been cut close to their insertion on that aponeurosis, and the entire muscle sheet, excepting the distal portion of the constrictor of the fourth arch ($Cs._6$), then turned downward to the level of the middle line of the gill openings. $\times\ 2$.

Fig. 10.—Lateral view of the constrictor and interbranchialis muscles of the third branchial arch of Mustelus. Dorsally, the continuous muscle-sheet formed by the constrictores superficiales has been cut along the line of the linear aponeurosis related to the arch, and also slightly posterior to that aponeurosis. Ventrally, the muscle-sheet has been cut immediately anterior to the line where the ventral portion of the constrictor of the arch ($Cs._5$) joins it, and also slightly posterior to that line. $\times\ 2\frac{2}{3}$